

The metabolic cost of birdsong production

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Summary

The metabolic cost of birdsong production has not been studied in detail but is of importance in our understanding of how selective pressures shape song behavior. We measured rates of oxygen consumption during song in three songbird species, zebra finches (*Taeniopygia guttata*), Waterslager canaries (*Serinus canaria*) and European starlings (*Sturnus vulgaris*). These species sing songs with different acoustic and temporal characteristics: short stereotyped song (zebra finch), long song with high temporal complexity (canary) and long song with high acoustic, but low temporal, complexity (starling).

In all three species, song slightly increased the rate of oxygen consumption over pre-song levels (1.02–1.36-fold). In zebra finches, the metabolic cost per song motif averaged $1.2 \mu\text{l g}^{-1}$. This cost per motif did not change over the range of song duration measured for the four individuals. Surprisingly, the metabolic cost of song

production in the species with the temporally most complex song, the canary, was no greater than in the other two species. In starlings, a 16 dB increase in sound intensity was accompanied by a 1.16-fold increase in the rate of oxygen consumption. These data indicate that the metabolic cost of song production in the songbird species studied is no higher than that for other types of vocal behavior in various bird groups. Our analysis shows that the metabolic cost of singing is also similar to that of calling in frogs and of human speech production. However, difficulties with measurements on freely behaving birds in a small respirometry chamber limit the depth of analysis that is possible.

Key words: song production, metabolic cost, song organization, oxygen consumption, zebra finch, *Taeniopygia guttata*, Waterslager canary, *Serinus canaria*, European starling, *Sturnus vulgaris*.

Introduction

During the breeding season, male passerine birds typically sing with great frequency. Song is thought to play a role in establishing and defending a territory and in attracting a mate. Singing rate and the acoustic characteristics of the song potentially provide information about the quality of the singing male. Singing rate may indicate the current physical condition of the bird, but also male quality in a more general sense, perhaps reflecting developmental conditions (e.g. Nowicki et al., 1998; Nowicki et al., 2000). Similarly, song quality may reflect learning and motor skills since learning plays an important role in song acquisition. Consequently, singing behavior should be subject to strong sexual selective forces (Searcy and Anderson, 1986; Searcy and Yasukawa, 1996).

A high singing rate may provide information about the fitness of the singing male in another way. Frequent singing takes time that could be spent on other types of behavior, such as foraging. A male that can afford to spend more time singing may be in possession of a high-quality territory, may be very efficient at foraging or may be otherwise in good physical condition. This notion is supported by the finding that birds provided with additional, easily available food have higher singing rates than controls without food supplements

(Ydenberg, 1984; Searcy, 1979; Gottlander, 1987; Strain and Mumme, 1988; Reid, 1987).

There is a direct cost associated with singing behavior. A number of motor systems contribute to song production (respiratory and syringeal musculature) and modification (upper vocal tract, beak movements) (for reviews, see Suthers and Goller, 1998; Suthers et al., 1999). Increased muscular activity requires energy, and singing must therefore increase the metabolic requirements of the male.

There has been some discussion about the costs of vocal behavior in birds (e.g. Eberhardt, 1994; Gaunt et al., 1996; Horn et al., 1995; McCarty, 1996; Jurisevic et al., 1999; Bachmann and Chappell, 1999). Eberhardt (Eberhardt, 1994) found that singing increased the metabolic rate of Carolina wrens (*Thryothorus ludovicianus*) up to ninefold over resting metabolic rate. In contrast, all other studies investigating the metabolic costs of generating vocalizations in birds showed much smaller, up to threefold, increases. These latter measurements included high-intensity vocalizations, such as crowing and distress calls (Gaunt et al., 1996; Horn et al., 1995), and begging of nestling birds (McCarty, 1996; Bachmann and Chappell, 1998; Jurisevic et al., 1999), but did

not include the song of passerine species. It is therefore reasonable to ask whether these reported differences in metabolic scope for different avian vocalizations are caused by an unusually high cost of song in passerines or whether other factors, such as methodological differences (see Gaunt et al., 1996; Eberhardt, 1996), may explain the variable results on metabolic cost.

More studies on the metabolic cost of singing in songbirds are needed to resolve this question. Furthermore, there is a need for comparative data, because songs vary greatly in their acoustic and temporal structure between species. It is possible that these differences may cause large variations in the metabolic costs of singing.

Some species sing short stereotyped songs that may be repeated a variable number of times in a song bout. One example is the song of the zebra finch (*Taeniopygia guttata*), which consists of 5–8 syllables. The acoustic structure of these syllables varies from simple harmonic stacks to frequency- and amplitude-modulated elements. Song is generated by rapidly switching between expirations and inspirations. Sound is typically produced during the expiratory phase, and syllables correspond to individual expiratory pulses. During intersyllable silent periods, short inspirations (minibreaths) are taken (Wild et al., 1998). This rapid switching between expiration and inspiration during song requires increased muscular effort, because expiratory and inspiratory pressures are obviously higher during singing than during quiet breathing.

Other species sing very long songs consisting of a number of syllables repeated in rapid sequence before switching to a new type. One extreme example is the Waterslager canary (*Serinus canaria*), which has been bred to enhance certain song features. Canaries sing long (up to 30 s) songs that consist of different trills with varying, but mostly rapid, pulse repetition rates. Rapid switching from expiration, during which phonation occurs, to inspiration (minibreaths) suggests that vigorous muscular activity is associated with song production. The expiratory and inspiratory muscles generate the appropriate pressure conditions, and the syringeal musculature is involved in gating airflow through the two halves of the syrinx (Hartley and Suthers, 1989; Hartley, 1990; Suthers, 1992).

Yet other species sing slow sequences of acoustically complex syllables, but song bouts may be several minutes long. Examples for this type of song organization are mimic thrushes (Mimidae) (e.g. Suthers et al., 1994) and European starlings (*Sturnus vulgaris*). Starlings generate a series of whistles interspersed with hisses and snarls (e.g. Eens et al., 1991a; Eens et al., 1991b). Many syllables are acoustically complex, but the song tempo is much slower than in zebra finches or canaries.

In addition, the sound amplitude generated by different species (Gaunt, 1987) may vary greatly. If one assumes vocal efficiency to be similar during soft and loud vocalizations, high-energy acoustic output must require increased energy expenditure. All these variables are likely to influence the metabolic cost of singing, illustrating the need for comparative data on songbirds.

We undertook such a comparative study by measuring oxygen consumption rates during song in three species. We selected the three species discussed above for their different song organization, zebra finches for short stereotyped songs, Waterslager canaries for long song duration with rapid trill rates and European starlings for acoustically complex songs with high-intensity differences within a song.

Materials and methods

Study animals

Adult males of three species were used in this study. Zebra finches (*Taeniopygia guttata*) were bred in our aviary and were more than 100 days old. Waterslager canaries (*Serinus canaria*) were purchased from a breeder and were more than 2 years old. European starlings (*Sturnus vulgaris*) were slightly over a year old and had been hand-raised the previous spring. Prior to the experiments, vigorously singing adult males were taken from the aviary to the experimental room and housed in a small cage (32 cm×24 cm×25 cm) to allow them to become accustomed to the new surroundings. Once the birds had resumed singing, they were placed into the metabolic chamber. All experimental procedures were approved by the Institutional Animal Care and Use Committee of the University of Utah.

Measurements of metabolic rate

An open-flow system was used to measure oxygen consumption. Room air was drawn through a metabolic chamber and an identical control chamber using an R-2 Applied Electrochemistry flow control unit. Air was dried (Drierite) and scrubbed of CO₂ (Ascarite) before it entered the analyzer. The percentage difference in oxygen content between the air in the two chambers was measured with an Applied Electrochemistry S-3A/2 oxygen analyzer (N 37M sensor). The metabolic chambers were either custom-made from plastic containers with an airtight lid (2.4 l for zebra finches and canaries, 10 l for starlings) or a small cage (30 cm×27 cm×25 cm, 20.25 l) was placed into a gas sampling bag (Tedlar) with gas inlet and outlet fittings (starlings). A unidirectional microphone (Optimus Dynamic Microphone) was attached to the lid of the plastic containers or was placed in front of the cage to record vocalizations in the metabolic chamber. The analog output voltage of the oxygen analyzer (percentage difference between the chambers) and the microphone recordings were stored on a multi-channel DAT recorder (TEAC RD 135).

For zebra finches, a little ‘window’ was the only transparent part of the metabolic chamber. The air outlet from the metabolic chamber to the oxygen analyzer was located at the base of this window. A perch was provided approximately 5 cm from the window. The air inlet to the metabolic chamber was at the back of the box. For canaries, the metabolic chamber had four outlets at the front and one inlet at the back of the chamber. The perch was located in the center of the box approximately 10 cm from the front wall. Starlings were placed in a larger container with a configuration similar to that of the

canary metabolic chamber. Only one starling would sing in this confined space, so we provided a larger 'metabolic chamber' by placing the holding cage into a gas sampling bag. In all experiments, food and water were provided in small dishes on one side of the chamber.

Oxygen consumption during singing was recorded between 08:00 and 19:00 h. All measurements were taken at room temperature (22–23 °C). Before each recording session, the sensor was calibrated with room air (20.95 % oxygen). The flow rate was kept at 880 ml min⁻¹, and all lines were as short as possible to optimize the temporal resolution of the system. Once calibration had been completed and the sensor reading had stabilized, a bird was placed in the experimental chamber. After an adjustment period of 20–30 min, recording was started. The birds were observed throughout the recording session. Zebra finches were recorded for up to 2 h. To stimulate singing behavior, a female was placed in front of the window. Canaries and starlings were recorded for up to 8 h. Singing was stimulated by playback of recorded conspecific song and by keeping subjects in acoustic and visual contact with other conspecific males and females.

The recordings were monitored on an oscilloscope (Hitachi VC-6645 digital storage oscilloscope). For every song bout, the counter number of the DAT recorder, the position of the bird in the metabolic chamber and information about its locomotor activity were recorded.

Resting metabolic rates (RMR) of all individuals were recorded at night during sleep (at a room temperature of 22–23 °C). The recordings were taken between 20:00 h and midnight, at least 1.5 h after the room lights had been turned off (the photoperiod of the room matched the local light:dark cycle). After calibration of the oxygen sensor to room air, a bird was placed in the box. Approximately 30 min after the lights had been turned off, the metabolic rate of the sleeping bird was recorded for at least 1 h. At the end of all recording sessions, the bird was taken out, and the metabolic chamber was allowed to re-equilibrate to room air. Differences in the oxygen content of the air from the two chambers at the end of the washout period were used to correct for sensor drift. Drift was typically very low and did not exceed 0.05 %.

The mass of all birds was determined to the nearest 0.1 g either prior to the measurements of resting metabolic rate or the following morning. In the case of the starlings, which could not be induced to sing in the small respirometry chamber for periods of up to 2 weeks, the mass was determined within days of the successful measurements during song to avoid significant changes in body mass during the course of the experiment.

Data analysis

Data were played back and digitized for computer analysis with Signal software (3.0 Engineering Design) using a DT-2821 AD board (Data Translation). Segments up to 200 s in length were digitized at a sampling rate of 2500 Hz. Only sequences during which the bird sat still for sufficiently long periods before and during the song were used for

measurements. The recorded oxygen values were corrected for standard conditions. Volumes of consumed oxygen (ml min⁻¹) were calculated following equations provided by Withers (Withers, 1977):

$$\dot{V}_{O_2} = \dot{V}_E(F_{IO_2} - F_{EO_2}) / (1 - F_{IO_2}),$$

where \dot{V}_{O_2} is the rate of oxygen consumption, \dot{V}_E is the rate of airflow out of the metabolic chamber, F_{IO_2} is the fractional concentration of O₂ entering the metabolic chamber and F_{EO_2} is the fractional concentration of O₂ leaving the metabolic chamber.

Oxygen volumes and microphone recordings were plotted, and the average rate of oxygen consumption was measured 10–20 s before song and during song. If pre-song measurements were not possible (when the bird moved during that period), we measured the rate of oxygen consumption for a 10 s period after the song, accounting for a 15 s period during which O₂ levels returned to baseline (see washout characteristics below). We refer to these measurements as average oxygen consumption (avg \dot{V}_{O_2}).

Song bouts are defined as singing behavior that was not interrupted by silences lasting more than 15 s. The total duration of the song bout (bout duration) was measured from the oscillogram of the microphone recording. Song duration is defined as bout duration minus the inter-song intervals and was determined using spectrograms calculated from the microphone recordings digitized at 40 kHz.

In the zebra finch experiments, a clear peak in the rate of oxygen consumption (see Fig. 1) was associated with each song bout. The volume of oxygen consumed for each song bout was calculated by subtracting baseline metabolic rate (i.e. the rate of oxygen consumption before or after song) and then integrating the remainder over time. We refer to these measurements as 'song O₂ volume'. In zebra finches, the average rate of oxygen consumption above the baseline value (i.e. avg \dot{V}_{O_2} during song minus avg \dot{V}_{O_2} before song) was also calculated. All metabolic measurements are presented as mass-specific rates of O₂ consumption (ml min⁻¹ g⁻¹) or mass-specific volumes (ml g⁻¹).

Assessing the temporal resolution of the system

The volume of the respirometer chamber is large in comparison with the flow rate, so the washout characteristics of each chamber were studied by injecting 1 ml pulses of nitrogen with a syringe (10 repetitions for each chamber). The syringe was connected to a narrow tube whose opening was positioned near the perch, simulating the position of the head of a bird when sitting on the perch and facing the outlet. This was to simulate criteria that were used to include song segments in the data analysis. For each pulse, the time from onset to peak and the time from peak to at least 98 % of baseline were measured. The average time to peak was 3.4 s for the 2.4 l container, 3.57 s for the 10 l container and 4.2 s for the 20.25 l container. The average time for return to baseline was 8.2 s for the 2.4 l container, 10.3 s for the 10 l container and 12.5 s for the 20.25 l container.

Statistical analyses

Differences in the average rate of oxygen consumption before and during song were tested with paired *t*-tests. Using a paired *t*-test allowed a more powerful comparison because the variability in the oxygen consumption rate before song was quite high, emphasizing the difference between silent periods and song. Linear regression analysis was performed using SigmaPlot 5.0 software.

Results

Zebra finches

When a female was placed in front of the transparent window, males typically perched on the other side of the window and sang spontaneously. Throughout the song bout, they remained on the perch and kept visual contact with the female. A distinct increase in \dot{V}_{O_2} was associated with each song bout. The oxygen analyzer registered this increase 2–4 s after the onset of song (Fig. 1), a delay attributable to the washout characteristics of the system.

Resting metabolic rates of the four zebra finches ranged from 0.089 to 0.119 ml O₂ g⁻¹ min⁻¹. During song, we measured average oxygen consumption rates (avg \dot{V}_{O_2}) of 0.106–0.305 ml O₂ g⁻¹ min⁻¹. Metabolic activity during song was significantly higher than before song (avg \dot{V}_{O_2} values before song ranged from 0.09 to 0.23 ml O₂ g⁻¹ min⁻¹; for average values for individuals, see Table 1).

The average \dot{V}_{O_2} before song was therefore 1.4–1.7 times resting metabolic rate, compared with 1.77–2.2 times resting metabolic rate during song. The factorial increase in \dot{V}_{O_2} from before song over during song was between 1.2 and 1.36.

Measurements of song O₂ volume indicate the added cost for singing one motif above that of baseline activity. Song O₂ volumes ranged from 0.45 to 2.3 μl O₂ g⁻¹ motif⁻¹ (average

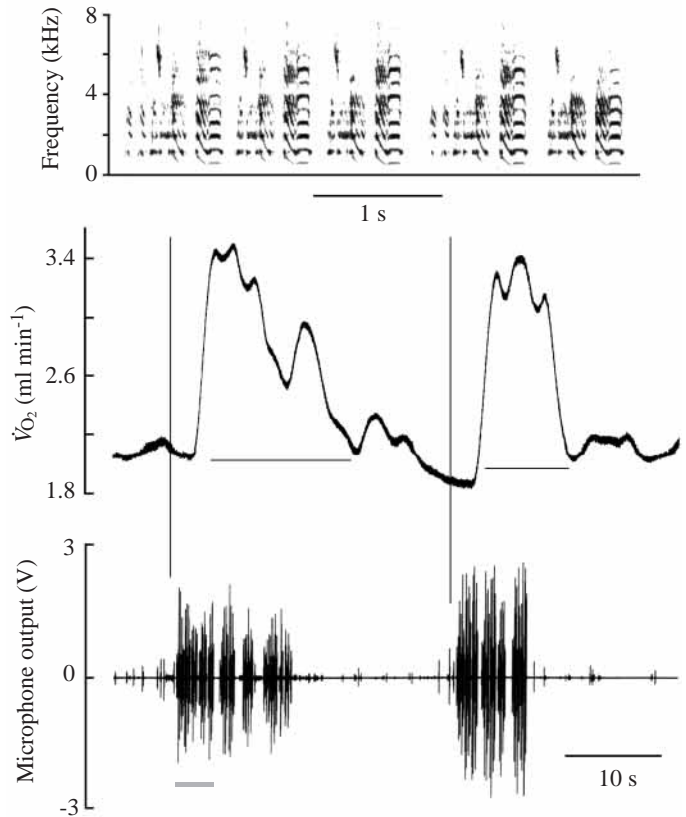


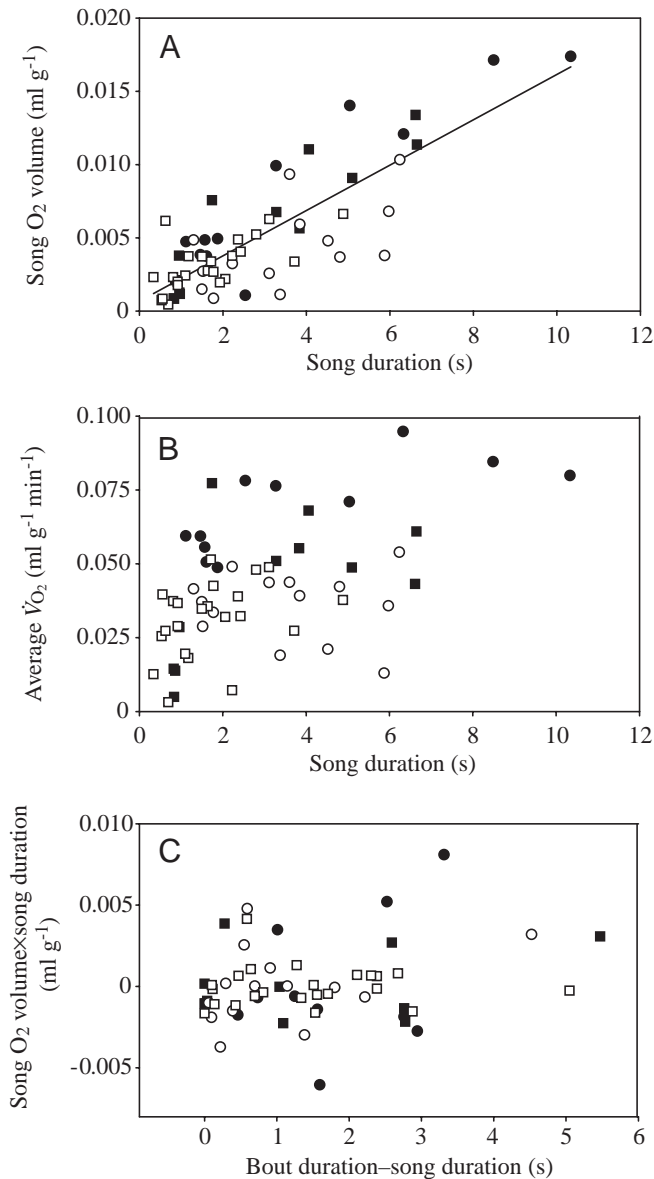
Fig. 1. Song bouts in zebra finches led to a distinct increase in the rate of oxygen consumption (\dot{V}_{O_2}). Song is shown as an oscillogram in the bottom panel. The segment indicated by the grey horizontal bar in the bottom panel is also shown spectrographically in the top panel. The central panel shows the rate of oxygen consumption, and the vertical bars illustrate the delay between the onset of song and the increase in the rate of oxygen consumption. Horizontal bars indicate the approximate level of pre-song metabolic rate.

Table 1. Rates of oxygen consumption during song in all individuals

Bird	N	Mass (g)	Rate of O ₂ consumption (ml g ⁻¹ min ⁻¹)			Factorial increase		Paired <i>t</i> -test, song/pre-song <i>P</i> -values
			RMR	Pre-song	Song	Song/RMR	Song/pre-song	
ZFR6	11	11.1	0.119	0.195±0.015	0.264±0.225	2.22	1.36	<0.001
ZFY13	14	11.4	0.093	0.129±0.024	0.165±0.034	1.77	1.28	<0.001
ZFY17	11	12.9	0.097	0.160±0.020	0.205±0.032	2.11	1.28	<0.001
ZFY21	22	13.2	0.089	0.154±0.022	0.185±0.028	2.08	1.20	<0.001
C114	12	18.8	0.057	0.136±0.015	0.139±0.016	2.44	1.02	<0.001
C125	24	19.0	0.058	0.121±0.019	0.127±0.019	2.19	1.05	<0.001
C62	38	18.8	0.040	0.084±0.009	0.087±0.01	2.18	1.04	<0.001
C71	10	18.3	0.039	0.129±0.017	0.133±0.018	3.41	1.03	0.0018
ST4	45	71.0	0.030	0.061±0.01	0.065±0.0085	2.17	1.06	<0.001
ST2	62	74.9	0.039	0.083±0.005	0.086±0.0052	2.20	1.04	<0.001
ST6	39	65.25	0.038	0.073±0.0057	0.079±0.0055	2.08	1.08	<0.001

Values are means ± S.E.M.

ZF, zebra finch; C, canary; ST, starling; N refers to the number of song bouts included in the analysis; RMR, resting metabolic rate.



$1.2 \mu\text{l O}_2 \text{ g}^{-1}$), with motif duration varying between the four individuals from 0.337 to 0.957 s (average 0.685 s). As expected, the song O₂ volume increased with song duration (Fig. 2A). Although the slope of this relationship suggests that the cost of singing a motif may increase with increasing bout length, this trend was not present when $\text{avg } \dot{V}_{O_2}$ during song was plotted over song duration for individuals (Fig. 2B). Although the slopes are slightly positive, they are not significantly different from zero.

Silent periods between the motifs of a song bout varied within and among individuals. The average duty cycle for song production during a song bout was $85 \pm 1.2\%$ (mean \pm s.d., $N=85$). This variability in duty cycle might account for a portion of the unexplained variance in the relationship between song O₂ volume and song duration. However, no significant relationship was found between silent periods within song bouts and the residuals of the song O₂ volume \times song duration

regression (Fig. 2C). The expected differences in \dot{V}_{O_2} caused by differences in duty cycle are probably beyond the resolution of these measurements.

Fig. 2. (A) The volume of oxygen consumed (V) increases with increasing duration (D) of song bouts (regression equation: $V=0.00069+0.00155D$; $r=0.82$; $F=125.9$; $P<0.001$). (B) The average cost of singing a song motif ($\text{avg } \dot{V}_{O_2}$ during song minus $\text{avg } \dot{V}_{O_2}$ before song) remains constant for the range of bout duration. Although the slopes of individual linear regressions are slightly positive for all four individuals, they are not significantly different from zero (t -tests on whether the slopes are different from zero yielded P -values of 0.336, 0.21, 0.42 and 0.11 for the four individuals). (C) The silent periods between motifs in a song bout do not explain much of the variance in A. Residuals from A (O_2 volumes \times song duration) are plotted over the difference between bout duration and song duration (i.e. the silent periods between song motifs). The regression is not significant ($F=2.53$; $P=0.117$), and the slope is not significantly different from zero ($t=1.59$; $P=0.1172$). In all three plots, different symbols indicate data contributed by the four individuals.

regression (Fig. 2C). The expected differences in \dot{V}_{O_2} caused by differences in duty cycle are probably beyond the resolution of these measurements.

Canaries

Canaries sang spontaneously in the metabolic chamber, and the duration of their songs ranged from 3 to 38 s. However, the position of the individuals within the respirometer chamber varied between song bouts, and movement unrelated to song also occurred frequently during song bouts. These movements caused fluctuations in \dot{V}_{O_2} that were of similar or greater magnitude than those associated with singing (Fig. 3), making it impossible to analyze many song bouts in more detail (i.e. in a manner similar to the analysis of the zebra finch data).

For the four individuals, resting metabolic rates ranged from 0.039 to 0.058 $\text{ml O}_2 \text{ g}^{-1} \text{ min}^{-1}$. The average \dot{V}_{O_2} during song ranged from 0.067 to 0.163 $\text{ml O}_2 \text{ g}^{-1} \text{ min}^{-1}$, whereas the average \dot{V}_{O_2} before song ranged from 0.064 to 0.157 $\text{ml O}_2 \text{ g}^{-1} \text{ min}^{-1}$. The average \dot{V}_{O_2} during each song differed significantly from the average \dot{V}_{O_2} before song (paired t -test, see Table 1, which presents average values for individuals).

The average \dot{V}_{O_2} before song was 2.1–3.2 times resting metabolic rate, compared with 2.19–3.4 times resting metabolic rate during song. The factorial increase in the average \dot{V}_{O_2} during song over the average oxygen consumption before song was 1.02–1.05.

Starlings

Only one individual (ST 4) sang in the small respirometry chamber (see Fig. 5), the other two males were recorded in the larger cage within the gas sampling bag (see Fig. 4). Because of the different volumes of the two arrangements used, the temporal resolution of the oxygen measurements differed between the two systems (Fig. 4; Fig. 5).

Song bouts of starlings were very long (20–30 min) and differed from those of the other two species in that the song was produced in loose sequences with silent periods between and was not organized into well-defined strophes. The singing behavior also differed between the three individuals. Starling

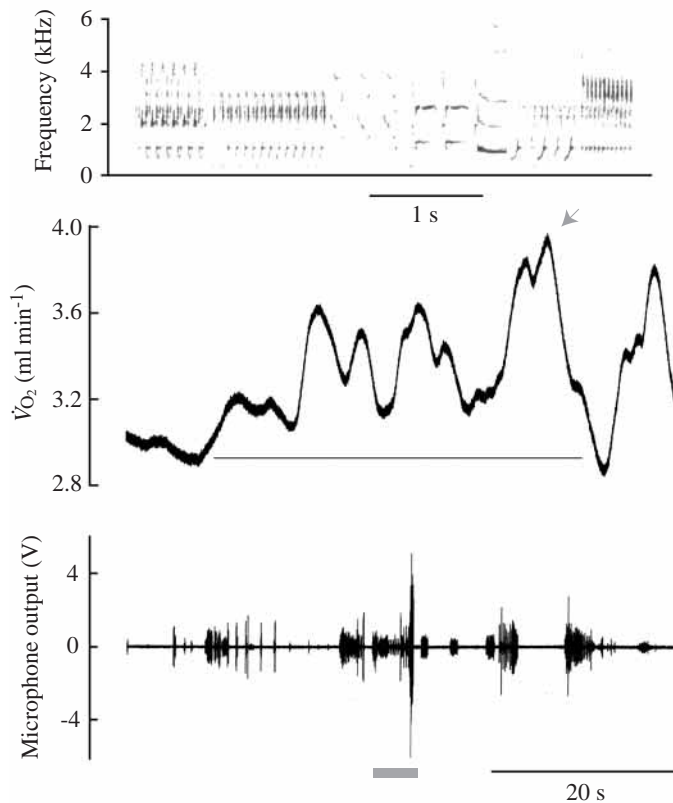


Fig. 3. Example of oxygen measurements during song from a canary. Song is shown as oscillogram (bottom panel). The segment indicated by the grey horizontal bar in this panel is also shown spectrographically in the top panel. The rate of oxygen consumption ($\dot{V}O_2$) is shown in the central panel. Note that the peak in oxygen consumption at the end of the song bout (indicated by an arrowhead) was caused by movement of the bird in the respirometry chamber.

ST4 sang loose sequences of soft whistles and then terminated a bout with a loud combination of snarls, hisses and whistles. The other two individuals did not show this striking distinction in sound amplitude between these categories of song (Fig. 4, Fig. 5).

Resting metabolic rates of starlings ranged from 0.030 to 0.039 ml O₂ g⁻¹ min⁻¹. Oxygen consumption rates before song ranged from 0.045 to 0.089 ml O₂ g⁻¹ min⁻¹ and increased significantly during song (range 0.046–0.095 ml O₂ g⁻¹ min⁻¹) (for average values for individuals, see Table 1). The average $\dot{V}O_2$ during song was therefore 2.08–2.17 times the resting metabolic rate and 1.04–1.08 times that before song.

The pronounced difference in sound intensity (16 dB) between the soft whistles and the terminal combination of song elements in ST4 was also expressed in the difference in the oxygen consumption rate (Fig. 5). In each song bout, the $\dot{V}O_2$ during soft song (0.056±0.0047 ml O₂ g⁻¹ min⁻¹, mean ± s.e.m., N=45) was lower than that during loud song (0.065±0.005 ml O₂ g⁻¹ min⁻¹, mean ± s.e.m., N=45). The difference was significant in a paired *t*-test (Table 2; *P*<0.001).

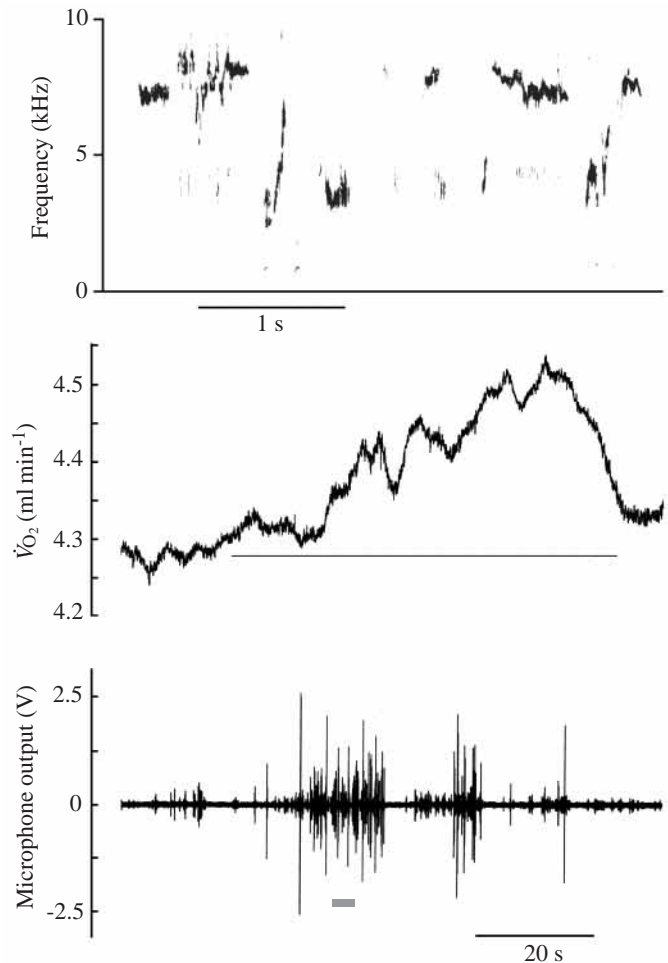


Fig. 4. Example of oxygen measurements during song by a starling in the large respirometry chamber. The rise in the rate of oxygen consumption ($\dot{V}O_2$) (central panel) is slow after the onset of song (indicated as oscillogram in the bottom panel). A segment of song (grey horizontal bar) is also shown spectrographically (top panel).

Discussion

In this study, we provide the first comparative data on the metabolic cost of singing in three passerine species. The data presented here allow a first assessment of the cost of phonation in comparison with other studies on avian vocal behavior. The song organization of the three species studied differs, so we will discuss the relationship between the metabolic cost and the temporal and intensity characteristics of song.

Resting metabolic rates

As shown in Table 3, the measured values for zebra finch RMR are consistently higher than standard metabolic rate calculated from an allometric equation for songbirds (Lasiewski and Dawson, 1967). Whereas the RMRs of canaries and starlings are generally in good agreement with the calculated values, measured values for zebra finches are approximately 1.5 times greater than calculated standard metabolic rates. A probable explanation for this discrepancy is the fact that zebra finches may not have been post-absorptive

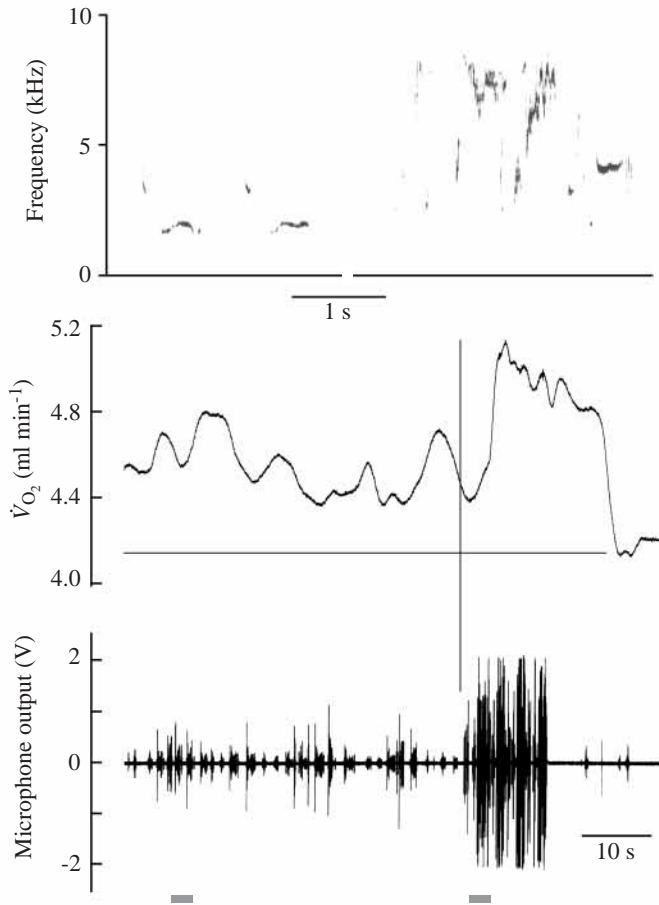


Fig. 5. Example of oxygen measurement during song by a starling in the small respirometry chamber illustrating the difference in the rate of oxygen consumption ($\dot{V}O_2$) between soft and loud song. Song is illustrated as an oscillogram (bottom panel), and two segments (horizontal grey bar) are also shown spectrographically (top panel). Note the more rapid response of the oxygen measurements (vertical line) than in the large respirometry chamber (see Fig. 4), as exemplified at the onset of the loud portion of song.

at the time we determined RMR 2 h after the lights had been turned off. Unlike starlings and canaries, zebra finches store considerable quantities of seeds in their crop, which may have prolonged their digestive phase in comparison with the other two species.

Comparison with other vocal behavior

We found that $\dot{V}O_2$ during song increased on average by 1.76–3.4-fold over resting metabolic rate (RMR) and by 1.05–1.38-fold over pre-song metabolic rate for all individuals measured in this study (Table 1). However, if we use calculated values for basal metabolic rate (BMR) in zebra finches, factorial increases range from 2.58 to 4.1 in that species. The increases over pre-song levels are within the range of measurements of metabolic rate increases associated with begging calls and distress calls in non-passerine and passerine birds (McCarty, 1996; Bachman and Chappell, 1998; Jurisevic et al., 1999). The metabolic cost of crowing in domestic roosters (*Gallus gallus domesticus*) and junglefowl (*Gallus gallus*), a vocal display with a similar functional use to passerine song, is similar (Horn et al., 1995) or even lower (Chappell et al., 1995) than that of song production, despite low efficiency (Brackenbury, 1977).

The only study investigating the metabolic cost of passerine song production, however, suggests substantially higher oxygen consumption rates during song than we measured. In singing Carolina wrens, mean factorial scopes (singing/RMR) ranged from 2.71 to 5.27 for four individuals (Eberhardt, 1994). While the lower mean values overlap with the range of factorial scopes in our study, the higher values exceed those measured here. In particular, the maximal value (8.7) measured for high singing rates (approximately 30 songs per minute) is well beyond the values reported here.

These high estimates of the metabolic cost of singing in Carolina wrens have been discussed extensively (e.g. Horn et al., 1995; Chappell et al., 1995; Gaunt et al., 1996; Eberhardt, 1996), and various biological and methodological reasons for the high measured metabolic rates during song have been offered. It was suggested that temporal and acoustic features

Table 2. Metabolic cost of soft and loud song in starling 4

Intensity range (V)	Average oxygen consumption during song ($\text{ml g}^{-1} \text{min}^{-1}$)		Factorial increase		Ratio loud/soft	
	Range	Mean	Song/pre-song	Song/RMR	Sound intensity	Rate of O_2 consumption
0.0255–0.0745 (soft)	0.051–0.067	0.056±0.0047	1.03	2.04	3.6086–9.4302	1.005–1.2293
0.1439–0.5347 (loud)	0.054–0.074	0.065±0.005	1.11	2.20	5.6699±1.84 ^a	1.16±0.0634 ^b

^aThis average difference corresponds to a 16 dB difference in sound intensity.

^b $P < 0.001$, paired t -test, average rate of oxygen consumption for soft song compared with rate of oxygen consumption for loud song. Values are given as ranges and as means \pm S.E.M. ($N=45$).

RMR, resting metabolic rate.

Table 3. Comparison of measured and calculated resting metabolic rates

Individual	RMR (kJ day ⁻¹) ^a	
	Measured	Calculated ^b
ZFR6	38.22	20.64
ZFY13	30.68	21.18
ZFY17	36.21	23.15
ZFY21	33.99	23.52
C114	31.02	30.40
C125	31.90	30.65
C62	21.77	30.40
C71	20.64	29.81
ST4	61.63	79.59
ST2	84.53	82.73
ST6	68.45	74.85

^aCalculated from oxygen consumption rates by assuming 20.1 kJ l⁻¹ O₂.

^bCalculated using the allometric equation for passerines from Lasiewski and Dawson (Lasiewski and Dawson, 1967).

RMR, resting metabolic rate; ZF, zebra finch; C, canary; ST, starling.

of passerine song in conjunction with small body mass may explain the difference from crowing or distress and from begging vocalizations (Chappell et al., 1995; Jurisevic et al., 1999). This interpretation can now be evaluated in the light of the data presented here. The song behavior of the species in our study is comparable with that of the wrens in duration and acoustic complexity. The long song duration of canaries matches the maximal recorded song rate of wrens. The temporal complexity of canary song, measured as trill rates, is greater than that of the song of Carolina wrens (see below). However, the rate of oxygen consumption during song is distinctly lower in canaries than that measured for high song rates in wrens.

As possible explanations for this discrepancy, we suggest the following points. Reporting the metabolic rate as a factorial increase over RMR fails to take into account that activity levels before song may be different among the species used in our study and the wrens. Our birds were either bred in captivity or hand-raised and kept in the laboratory for at least 1 year, whereas the wrens were caught only weeks before the experiment. It is likely that the general activity level of wild-caught specimens is much higher in a confined space than that of birds accustomed to captive conditions. Data on pre-song rates of oxygen consumption are not available for the wrens. In addition, locomotor activity other than song may cause increased metabolic rates that exceed the increases caused by song. Activity levels of wrens were not monitored (Eberhardt, 1994; see also Gaunt et al., 1996) but, as our observations of movements by canaries show, hopping or wing flapping shortly before or during a song bout might significantly distort measurements of song metabolic rate.

Methodological considerations

In general, measuring $\dot{V}O_2$ during song in birds behaving normally is challenging. The volumes of the respirometry chambers used need to be sufficient to get birds to sing, but large volumes reduce the temporal resolution of the system, potentially introducing errors into the metabolic measurements. In the present study, we attempted to escape this dilemma by placing the perch near the connection to the analyzer and setting criteria for the position and behavior of the bird for inclusion of measurements in the analysis. The calibration of temporal resolution indicates that, using this technique, we improved the response time of the system such that it was sufficient for the dynamic nature of song production in the three species. However, because of these circumstances, it was only possible to measure a quasi-steady-state metabolic rate during song in the two larger respirometry chambers. Given the long and intermittent nature of song bouts, this method was the best compromise for estimating the metabolic cost of singing. Other methods that take washout characteristics into consideration are difficult to employ because ongoing behavior interferes with measurements during the long washout period. By comparing the estimates from direct determination of the oxygen volume with the average $\dot{V}O_2$ of zebra finches, we can evaluate the accuracy of the system used here. Volume data yield a metabolic rate 1.3 times higher than the values estimated by averaging (Fig. 2A; Table 1). This increase might indicate that averaging underestimates the cost of singing in zebra finches by this factor. Alternatively, it may reflect the fact that the slope of the regression (Fig. 2A) is somewhat overestimated by the small number of data points for long song duration contributed by birds with higher song metabolic rates. Because canaries and starlings typically sing much longer song bouts, we expect the averaging to give more reliable estimates of the metabolic rate during song in these species.

Song organization, song intensity and metabolic rate

The two main muscle systems involved in song production, the syringeal muscles and the respiratory muscles (Suthers et al., 1999), probably account for a large proportion of the direct energetic demands of song behavior. In particular, respiratory activity during song may be the most energy-demanding motor component (Gaunt et al., 1996). Expiratory muscles generate the pulses of elevated pressures required for song production. Most songbirds insert short inspirations (minibreaths) between song syllables, which requires reconfiguration of the respiratory system from expiration to inspiration and back to expiration for each sound pulse and silent interval (Wild et al., 1998). Rapidly trilled phrases with minibreaths should, therefore, be particularly costly to produce (Suthers and Goller, 1998).

The syringeal muscles are also activated during song to control the airflow and the acoustic structure of the sound. For example, the activity of the largest syringeal muscle, *m. syringealis ventralis*, increases exponentially with increasing fundamental frequency of the ipsilaterally generated sound

(Goller and Suthers, 1996b). Similarly, at the onset of each vocalization, the syrinx is partially adducted by dorsal muscle action. During lateralized sound generation, the silent-side contraction of the dorsal muscles completely closes the syrinx. In contrast, the syrinx is typically abducted (*m. tracheobronchialis ventralis*) to maximize inspiratory airflow during minibreaths (e.g. Goller and Suthers, 1996a).

Taking into account respiratory and syringeal muscle activity, canary song should be more costly than either zebra finch or starling song because of the rapid trill rates of canary song (e.g. Hartley, 1990) and the exceptionally long song duration. This is not, however, what we found. The factorial increase (song/pre-song) in the metabolic rate was greatest in zebra finches (1.2–1.36) and did not differ between canaries and starlings. It would be interesting to know whether the extreme lateralization of sound production in canaries might reduce the power requirements and, thus, explain the low oxygen consumption rates. Waterslager canaries sing more than 90% of the syllables on the left side of the syrinx while closing the silent right side to airflow (Nottebohm and Nottebohm, 1976; Hartley and Suthers, 1989; Hartley and Suthers, 1990; Suthers 1992; Suthers and Goller, 1998). However, whether unilateral phonation is more efficient than bilateral phonation remains unclear.

A possible explanation for the low cost of canary song may be found in sound intensity differences. The production of sounds with a higher sound pressure level requires more energy assuming that the efficiency of energy transformation remains constant. Although we could not measure sound pressure levels reliably under our experimental conditions, canary song is typically softer than that of zebra finches or starlings. This qualitative observation is also confirmed by published measurements of sound intensity for canaries (79 dB), which is at the lower end of the range of intensities reported for songbirds (Gaunt, 1987). In starling 4, the metabolic cost of intensity variation could be measured reliably. A 16 dB difference between loud and soft song led to a 16% increase in the rate of oxygen consumption (Table 2). Given the wide range of sound intensities reported for different songbird species (74–100 dB) (Gaunt, 1987), substantial variability in the cost of singing behavior can be expected. However, factorial increases of up to 8.7, as reported for the Carolina wren (Eberhardt, 1994), probably cannot be explained by intensity differences. These findings do suggest, however, that our estimates of the metabolic cost of singing may be low if extrapolated to birds in their natural habitat. It is likely that birds in our respirometry chambers sang less loudly than birds in normal behavioral situations.

Comparison of the cost of phonation among taxonomic groups

Comparisons of the metabolic cost of phonation among taxonomic groups are problematic. For example, the energy requirements for phonation in birds have been compared with the cost of acoustic mating signals in frogs and insects, the two acoustic communication systems whose energy demands have

been studied in most detail (for a review, see Ryan, 1988). Comparisons of energy requirements between birds and frogs are usually based on the factorial increase in phonatory metabolic rate over RMR (e.g. Eberhardt, 1994). Average factorial increases in calling frogs are typically more than 10-fold and can be as high as 20-fold (e.g. Taigen and Wells, 1985). Frogs, however, are ectotherms, suggesting that these high values of factorial increase can be at least partially attributed to a low RMR.

Comparison of the actual volume of oxygen needed to produce acoustic signals may be more meaningful. The absolute metabolic cost of calling ranges from 1.8 to $4.79 \mu\text{l g}^{-1} \text{s}^{-1}$ in five species of *Hyla* (Prestwich et al., 1989). Interestingly, these values are similar to the average cost of song production in zebra finches, for which comparable data are now available. For 1 s of song, we measured an increase in oxygen volume of $2\text{--}3 \mu\text{l g}^{-1}$ over that during the pre-song period.

The cost of song production in songbirds is lower than that measured for the production of echolocation calls by stationary bats. Metabolic rate increases to $9.5\times\text{RMR}$ in pipistrelle bats (*Pipistrellus pipistrellus*) at pulse repetition rates of 10 Hz (Speakman et al., 1989). However, during flight, echolocation calls add no measurable cost to that of flying (Speakman and Racey, 1991).

It is also interesting to compare song production in birds with the metabolic cost of speaking in humans. Rates of oxygen consumption during a reading task at three different sound pressure levels were compared with values during quiet breathing (Russell et al., 1998). At low sound pressure levels (88 dB for men), rates of oxygen consumption decreased significantly compared with quiet breathing before the reading task, stayed the same during reading at comfortable sound pressure levels (93 dB for men) and increased (1.19-fold for men) for reading at high sound pressure levels (103 dB for men). However, during reading at low sound pressure levels, there was an oxygen debt that was repaid by increased expiratory volume and a higher oxygen consumption rate immediately after the reading task. The absence of an increase in energy expenditure during comfortable speech is thought to come at the expense of acid–base homeostasis (Russell et al., 1998).

Although it is difficult to make direct comparisons, the overall cost of birdsong production and speaking loudly are similar. The 19% increase from quiet breathing or comfortable speaking to speaking at high sound pressure levels is comparable with the increases measured for song production in our birds (Table 1, Table 2). The human study suggests that speaking may result in an oxygen debt under certain breathing conditions. We did not find increased oxygen consumption rates after song bouts in any of our birds, suggesting that the respiratory patterns of song did not generate an oxygen debt. However, the fact that the birds often moved around upon completion of the song bout prevented us from looking for oxygen debt systematically.

This study presents the first comparative analysis of the

metabolic cost of song production in songbirds. The data suggest that song production causes small but distinct increases in rates of oxygen consumption in all three species. More comparative data are needed to investigate the relationship between metabolic cost and song organization. Future studies should also focus on the relationship between sound intensity and metabolic cost. Considering the substantial methodological difficulties with freely behaving birds in open-flow respirometer chambers, future studies would benefit greatly if some of these problems could be circumvented by the application of a mask system.

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