

## OXYGEN CONSUMPTION DURING SINGING BY MALE CAROLINA WRENS (*THRYOTHORUS LUDOVICIANUS*)

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**ABSTRACT.**—A technique was developed to measure oxygen consumption during singing in captive male Carolina Wrens (*Thryothorus ludovicianus*). Oxygen consumption during singing varied between individuals, which may have been a result of variation in singing rates. The average basal rate of metabolism was estimated to be  $3.31 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  from standard metabolism measurements made at night. Oxygen consumption during singing ranged from  $9.07$  to  $28.69 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ . Captive study animals used singing rates similar to wild wrens. A comparison between metabolism during singing and resting showed that the cost of singing in male Carolina Wrens is higher than the costs of other common activities of passerines except flight. Received 31 July 1992, accepted 25 November 1992.

BIRDS USE SONG to attract mates, repel rivals, and maintain social contact (Krebs et al. 1978, Catchpole 1982, Ritchison 1983, McDonald 1989). These potential benefits of singing have associated costs. Because singing necessitates muscular contraction (Brackenbury 1980, Gaunt and Gaunt 1985), energy is expended to produce sound. The energy expenditure of singing may reduce body reserves and threaten survival (Clutton-Brock and Albon 1979, Robertson 1986), or have long-term effects by accelerating senescence (Partridge and Harvey 1985). Thus, an understanding of the amount of energy required for singing helps to predict when birds will take advantage of the benefits of this acoustic display.

Theories of sexual selection predict that mate choice will lead to the evolution of costly displays that indicate the health or condition of displayers (Grafen 1991). Singing may have evolved through mate attraction as an expensive display that only vigorous males can perform well. Wells and Taigen (1986) found that the high cost in energy expenditure of calling in one species of frog, *Hyla versicolor*, influences calling rate and duration because the frogs reach a physiological limit in calling effort. Sage Grouse (*Centrocercus urophasianus*) mate-attraction displays also have energy demands near physiological limits (Vehrencamp et al. 1989). However, grouse perform elaborate displays that involve more than just sound production. Although studies have shown that singing functions in mate attraction (Catchpole 1982, McDonald 1989), the question of whether or not bird song is energetically expensive remains

unanswered because few direct measurements of singing birds are available.

Three lines of evidence suggest that bird song can be limited by energy needs: (1) Song output increases when birds are provided with supplemental food (Searcy 1979, Gottlander 1987, Reid 1987, Strain and Mumme 1988). (2) Cold ambient temperatures reduce singing rate (Garson and Hunter 1979, Higgins 1979, Santee and Bakken 1987). (3) Muscle exhaustion during singing may lead to song switching (the anti-exhaustion hypothesis; Lambrechts and Dhondt 1988). None of these observations provides enough conclusive evidence for a high cost of singing, but taken together, suggest that the energetic cost of singing may limit song production.

Direct measurements of energy expenditure during singing are difficult to make. Measurements of the energy expenditure of free-ranging birds would provide the most valid data on singing. However, the doubly-labeled-water field technique (Weathers et al. 1984) cannot detect the short-term energy expenditure of free-ranging birds during the relatively brief duration of a song. Telemetry of heart rate, another field technique, has been used to study duck behavior, including quacking (Wooley and Owen 1978), but the relationship between heart rate and energy consumption has not been clearly established (Goldstein 1988). Thus, laboratory methods of measuring energy consumption like those used with frogs and insects (Stevens and Josephson 1977, MacNally and Young 1981, Prestwich and Walker 1981, Bucher et al. 1982, Taigen et al. 1985, Wells and Tai-

gen 1986, Lighton 1987, Prestwich et al. 1989) are necessary for determining the true cost of bird song.

Laboratory methods include the difficult task of inducing birds to sing in a confined space. In this study, I developed a method to persuade male Carolina Wrens (*Thryothorus ludovicianus*) to sing in a metabolic chamber. I measured their energy expenditure in the form of oxygen consumption at different rates of singing. Carolina Wrens were chosen because they are common, are easily captured and kept in captivity, are passeriforms with a complex song, and are known to sing in captivity (Simpson 1984).

#### METHODS

*Wren capture and maintenance.*—Wild male Carolina Wrens were captured in mist nets on the University of Florida campus, Alachua County, Florida, 1988 and 1989 while using playbacks of male songs as an attractant. After a laboratory acclimation period of three to five days, rates of metabolism were measured as oxygen consumption during both resting and activity for each individual. During acclimation and measurement, wrens were kept on a natural photoperiod at room temperature (23°–28°C). Food consisted of both *Tenebrio* sp. larvae (mealworms) and a meat mash mixture (cooked lean beef, cooked egg, carrot, and chick feed in a 2:2:2:3 ratio). When measurements of metabolic rates were completed, each individual was released back to his territory, usually within three weeks of capture.

*Basal-metabolism determination.*—I made measurements of standard metabolism of Carolina Wrens and used these to calculate basal metabolism, which previously had not been determined for this species. Standard metabolism measurements were made after dark on resting wrens at different temperatures (16.0°–37.1°C) using an Applied Electrochemistry S3-A oxygen analyzer and a Honeywell Elektronik 196 chart recorder in an open-flow-respirometry system. A sealed 2-L plastic jar immersed in a Forma Scientific water bath (model 2425) was used for most of the night measurements to allow close control of temperatures. Some standard rates measured at room temperature were made in the 13.7-L “behavior” chamber described below. Air was pushed through the 2-L chamber at flow rates of 200 to 500 cm<sup>3</sup>·min<sup>-1</sup>. Air-flow rate was measured (with a Brooks Sho-rate flowmeter calibrated with a Brooks volumeter) after carbon dioxide and water vapor were removed with soda lime and silica gel, respectively. The 2-L chamber and the behavior chamber yielded identical metabolic rates when both were used at the same temperature; thus, wrens were reaching a similar resting state in both systems.

Each nightly run was continued until a wren had

reached a quiescent period 2 to 3 h after the onset of darkness and metabolism (oxygen consumption) had reached a stable, constant rate. Wrens were not deprived of food prior to runs, but by the end of each run they had not eaten for at least 2 h. Body temperature was measured at the end of each run with a thermocouple probe inserted at least 1 cm into the cloaca. Oxygen-consumption rates (McNab 1978) and thermal conductance based on body temperature (McNab 1980) were used to determine the lower end of the thermal neutral zone and the basal rate of metabolism.

*Measurements of energy expenditure during singing.*—Metabolism during singing was measured in a 13.7-L chamber. Air was pulled through this behavior chamber using an Applied Electrochemistry Ametek R-2 flow-control air pump. Air flow rates of 500 to 700 cm<sup>3</sup>·min<sup>-1</sup> were used and measured as above. These flow rates allowed adequate flushing because they fell above the critical air flow rate for the chamber (as described by McNab 1988).

The behavior chamber (19 × 19 × 38 cm) was made of 4-mm clear-plexiglass sheets sealed with silicon. The entire front plexiglass sheet acted as a door and was unbolted and replaced with screen when oxygen-consumption measurements were not being made. Three sides and the ceiling of the chamber were lined with 1-cm-thick polyurethane for acoustic damping. The light from a 60-watt incandescent bulb, which passed through a 5% solution of copper sulfate to absorb heat, lit the chamber from outside. Four perches at different heights and *ad libitum* food and water were provided to each wren in this chamber when metabolic measurements were not being recorded. The chamber was artificially ventilated at all times. Each wren was acclimated to the confined space by being housed continuously in this chamber for up to seven days.

Efforts were made to induce singing by playback of other male wrens' songs and/or visual contact with a second wren, but these were unsuccessful. However, when some individual wrens were housed continuously in the chamber for two to three days, they began to sing spontaneously in the chamber each morning. I made oxygen-consumption measurements of this spontaneous singing from early to midmorning.

Because most singing bouts lasted for only a short period of time, oxygen content of the chamber could not reach an equilibrium during singing. Thus, the method described by Bartholemew et al. (1981) for making instantaneous measurements of oxygen consumption of short-length behavior patterns was employed for analyzing singing bouts. Measurements of the effective volume of the chamber were made using the temperatures and flow rates of the singing trials.

Rates of singing were quantified during the metabolism measurements. Singing rate was measured as the number of songs/minute. A song was defined

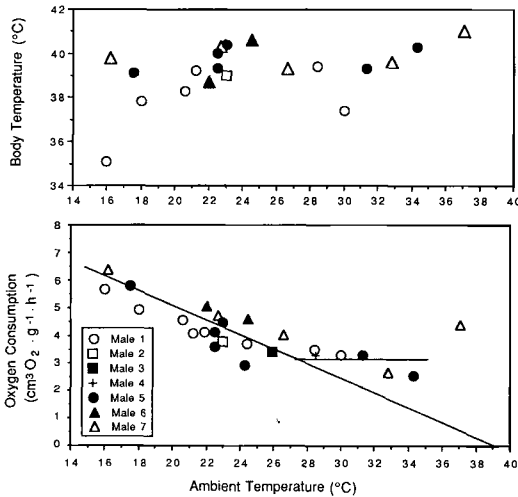


Fig. 1. (A) Cloacal temperature and (B) rate of metabolism as function of ambient temperature for seven male Carolina Wrens. Thermal conductance calculated using body temperature (McNab 1980). Critical temperature at lower end of zone of thermal neutrality estimated to be 27°C.

as one series of phrases or "tea kettles" (as described by Borror 1956). Singing rate was compared to the change in metabolism due to singing with a Spearman's rank correlation coefficient.

## RESULTS

Metabolic rate changed with ambient temperature as expected for five individuals ( $\bar{x} = 19.4$  g) measured at night (Fig. 1). Average thermal conductance was calculated to be  $0.28 \pm 0.06$   $\text{cm}^3 \text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot \text{°C}^{-1}$  ( $n = 17$ ). The lower boundary for the thermoneutral range of temperatures was estimated to be 27°C. Below this temperature the wrens increased metabolic rate to maintain their high body temperature that averaged  $39.4 \pm 0.91$ °C ( $n = 19$ ). Basal metabolism was the average metabolic rate recorded in the thermoneutral zone,  $3.31 \pm 0.30$   $\text{cm}^3 \text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  ( $n = 7$ ). This basal rate falls within the expected range of other passerines of this size (Lasiewski and Dawson 1967).

Only 4 of 20 wrens used sang spontaneously in the metabolic chamber during a time I was measuring oxygen consumption. Three of these four were birds of the year that had been captured and were measured in late summer and early fall, while the fourth was an adult bird captured as a bird of the year and held in captivity until measurements were made the fol-

TABLE 1. Mean oxygen consumption and factorial scopes ( $\pm$ SE) during singing for four male Carolina Wrens.

Male	<i>n</i> (song bouts)	O <sub>2</sub> consumption during singing ( $\text{cm}^3 \text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ )	Factorial scope (singing/ standard metabolism)
1	2	$9.93 \pm 0.90$	$2.71 \pm 0.24$
2	4	$19.99 \pm 3.03$	$5.27 \pm 0.80$
3	3	$10.92 \pm 0.29$	$3.22 \pm 0.09$
4	1	10.59	3.25

lowing spring. Singing occurred only in the morning within 3 h after sunrise.

Metabolism ranged from 9.07 to 28.69  $\text{cm}^3 \text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  during singing while the birds sang in the chamber at rates of 7.5 to 32.0 songs/min. Oxygen consumption rates differed among the three individuals (Kruskal-Wallis,  $H = 6.11$ ,  $P = 0.0471$ ). The fourth individual was not included in this analysis because of a low sample size (Table 1). The factorial scope for singing was calculated using the standard metabolism (SMR) of each wren at the same ambient temperature as used in the singing trials and ranged from 2.71 to 5.27 SMR. Oxygen consumption increased with song rate (Fig. 2; Spearman's rank correlation,  $n = 9$ ,  $P = 0.059$ ).

## DISCUSSION

The average oxygen-consumption rate during singing differed between individual birds. This variation could be a result of age differences because the three young birds all had higher energy expenditures than the adult male (Male 1). However, Male 2 had particularly high values, even when compared to the other young birds. Because Male 2 also had higher singing rates than the other three males, I looked for a correlation between singing rate and energy expenditure. When singing bouts for which I had singing rates were combined for all individuals and compared to oxygen-consumption rates, I found a positive correlation. While repeated measurements on the same individuals make this test about singing rate inconclusive, it is clear that oxygen consumption always increases during singing and that opportunities for selection may arise because of individual variation in this energy expenditure.

My data suggest that wrens must increase their energy expenditure with an increase in time

spent singing and possibly in singing rate. This elevated cost of a greater song output may result in a decreased singing rate if wrens are energy stressed. Under such conditions, males with greater energy reserves should be able to sing more than males with fewer reserves. Advertisement that indicates the health and vigor of the singer is predicted to evolve both through female choice of high-quality mates and intra-sexual selection in territorial defense (Grafen 1991). Given that more singing has a higher cost, one would expect to see females choose males that sing more or sing faster, and indeed the results of many studies of birds support this prediction (Payne and Payne 1977, Grieg-Smith 1982, Gottlander 1987, Reid 1987, Reid and Weatherhead 1990, Möller 1991).

Based on my findings of increased energy consumption with more sound production, I suggest that elaborate songs are likely to cost more than simple ones because production of elaborate songs usually requires the use of longer phrases (Kroodsma 1977). If elaborate songs are more energetically demanding, sexual-selection theory predicts that female choice would lead to elaboration of songs, as well as to a faster rate of singing. Such a trend toward more elaborate songs in polygamous species where selective pressures on males from female choice are most intense has been observed in both wrens and warblers (Kroodsma 1977, Catchpole 1980). Thus, my data may explain why elaborate songs are common in polygamous species.

One way to determine the cost of singing in terms of energy expenditure for Carolina Wrens is to compare the cost to a basal energy expenditure. Vehrencamp et al. (1989) and Wells and Taigen (1986) compared the metabolic rate during acoustic display to resting metabolism and concluded that physiological limits were reached during display in grouse and frogs, respectively. I found that singing wrens consumed 9.07 to 28.69  $\text{cm}^3 \text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ . Thus, energy consumption increased 2.74 to 8.66 times basal metabolic rate ( $3.31 \text{ cm}^3 \text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) for singing adult wrens. These values are less than the 11-times basal rate reported for sustained flight in other species (Goldstein 1988) and much less than the cost of brief flight in a small passerine that was estimated at 23 times the basal rate of metabolism (Tatner and Bryant 1986). Assuming that these values for energy expenditure during flight can be generalized to other unmeasured species such as Carolina Wrens,

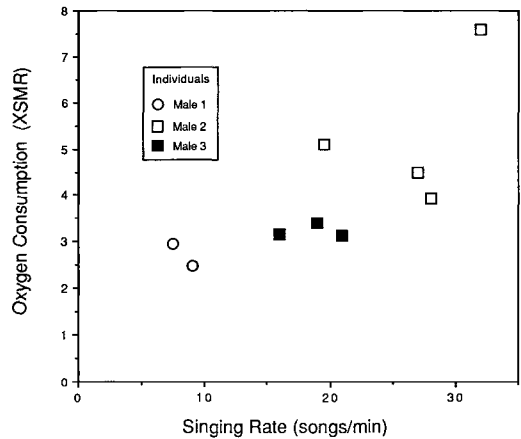


Fig. 2. Relationship of energy expenditure and singing rate for three Carolina Wrens. Male 1 was an adult bird; Males 2 and 3 were immature birds.

energy expenditure during flight can be much higher than levels reached during singing and, thus, singing wrens are not reaching their physiological limits. However, my measurements for singing are higher than those reported for some other common avian activities including perching (1.0–2.1 BMR), eating (1.7–2.2 BMR), gliding (2.0 BMR), and preening (1.6–2.3 BMR; see Goldstein 1988). If measurements on other taxa can be extrapolated to Carolina Wrens, then singing appears to be more costly than most other typical activities for wrens except flight.

Ideally, this information on the cost of singing for Carolina Wrens can contribute to construction of a complete time/energy budget of wild wrens. Morton (1982) reported enough information on the singing behavior of one male Carolina Wren during March in Maryland to construct a simple energy budget. This wren spent 3.86 h singing and 8.14 h engaged in nonsinging behavior during observations. Assuming that

$$E_{\text{Total}} = E_s T_s + E_{ns} T_{ns} \quad (1)$$

where  $E$  represents the energy expended,  $T$  the time spent in performing an activity, and  $s$  and  $ns$  denote singing and nonsinging activity, respectively, then an estimate of the increase in energy required to sing can be estimated. I used a combination of Morton's time data, my measurement for cost of singing, and a range of costs for other nonsinging behaviors to determine what percentage of the total energy budget is attributed to singing. For the purposes of

this estimate I assumed that the wren's non-singing behavior was split evenly between flight (23 BMR) and perching (2 BMR). By using both the maximum and minimum values of the cost of singing from this study, I calculate that singing accounts for 9.4 to 24.7% of the total energy budget of this wren. The calculations provide a range of possibilities for the way singing contributes to the total energy budget of Carolina Wrens; however, detailed time budgets are needed for more precise calculation of energy allocation. Such energy budgets would indicate the significance of the increased energy usage during singing in relation to the total energy requirements of the organism. Knowing the percentage of energy needed to support singing will help determine whether birds must curtail their singing (and, thus, territoriality and/or mate attraction) during periods of energy limitation.

Although I measured singing in only four individual Carolina Wrens, this is the most detailed research to date on the cost of singing in passerine birds. I found a clear increase in energy consumption during singing that most likely was a result of the muscle contractions necessary to produce song. One group of muscles that could contribute to this energy expenditure is the set of small muscles that control the configuration of the syrinx (Gaunt and Gaunt 1985). If these muscles contribute greatly to the total energy consumption, one would predict that the cost of different song types in a bird's repertoire would vary widely because the musculature of the syrinx determines exactly what types of sounds are made by this structure (Ames 1971). This idea would lend support to the anti-exhaustion hypothesis of Lambrechts and Dhondt (1988): if different sets of muscles are used for each song type in an energy-intensive manner, a bird would be expected to switch song types to avoid exhaustion. In the birds that I measured, the three young birds consumed more oxygen than the adult bird during singing. One distinctive characteristic of the song of young birds is frequent switching between song types. Perhaps the greater energy expenditure of young birds reflects the use of more muscles by these inexperienced singers. Clearly, more research is needed on energy consumption during singing, including comparisons of different songs in a bird's repertoire and different types of singing.

Although captive wrens used similar singing

rates to wild wrens (9 song/min, Simpson 1984), they never sang in the same posture as wild wrens. When males sing in the wild on their territories, they usually tip their heads back, fluff throat feathers, and visibly open their beaks. At no time during any of the spontaneous singing in the metabolic chamber did I observe this full-singing posture. I have measured the cost of producing sound for male wrens. However, my results may be conservative estimates of the cost of the type of singing that wrens appear to perform on their territories.

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