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Energy Expenditure During Singing: A Reply to Gaunt et al.

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A recent commentary by Gaunt et al. (1996) contains some interesting points about my paper on oxygen consumption of Carolina Wrens (*Thryothorus ludovicianus*) during singing (Eberhardt 1994). Here, I address some of their comments. After the appearance of my paper, several studies reported the energetic cost of sound production in nonpasserines (Chappell et al. 1995, Horn et al. 1995). To my knowledge, however, no additional studies have been reported of energy expenditure during singing in passerines. This fact, combined with the dialog in these commentaries, underscores the need for more research on the costs of singing in passerines.

Theoretical framework of original paper.—In the introduction of my original paper, I tried to place the use of information on the energy expenditure of birds during singing into a broader context. This included the fact that some theories of sexual selection predict

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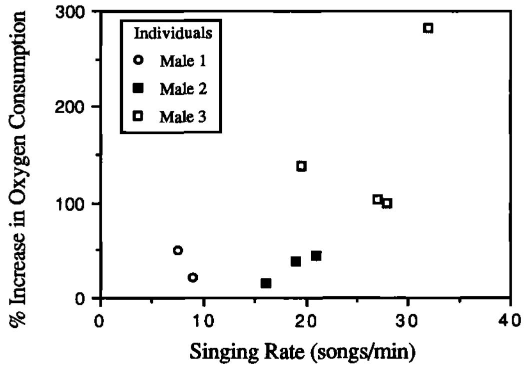

Fig. 1. Relationship of the percent increase in oxygen consumption and singing rate for three male Carolina Wrens. Percentage change in oxygen consumption was measured between prior non-singing behavior and each singing bout.

that a high cost will be associated with a display. This cost may include energy expenditure, and the display may include singing. However, not enough is known to assume that a high energy expenditure will be associated with singing. In addition, the observations that I cited suggest a possible energetic cost to singing, but by no means are they conclusive of this. Indeed, as I stated in the original paper (p. 124): "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." Gaunt et al. seem to misinterpret my effort to emphasize the possibility of a high energetic cost for singing and view it as a conclusion rather than an intriguing unknown that lacks concrete evidence. My purpose simply was to underscore the need to obtain direct measurements of energy expenditure in singing birds.

In their discussion of my original paper, Gaunt et al. seem to assume that singing will be associated with a very low energy expenditure. For example, they state "Sound displays allow the permeation of a large, but reasonably defined, possibly complex, volume with little change in location of the sender and, thus, *little overall energy expenditure*" (emphasis mine). This kind of unsubstantiated conjecture, common in much of the literature that addresses the potential costs of singing, is exactly what I had hoped to begin to address with my measurements on wrens. It also sends a cautionary message about the authors' critique of my results. In my paper, I do not attempt to claim that the energy expenditure that I measured during singing is either high or low. Instead, I simply report my findings and suggest some ways that the data could be applied to time budgets if more information were available. I also try to suggest how these data lead to further questions concerning repertoire size and singing rate. Gaunt et al. apparently assume that I have shown a particularly high energetic cost to singing and that this cannot be possible given the few tidbits we know about costs of nonpasserine vocalizations (e.g. Chappell et al. 1995, Horn et al. 1995). Despite my data from Carolina Wrens and the new information from roosters, I believe we still lack adequate information to determine whether singing is either very costly or negligible for passerines.

Methodology.—Gaunt et al. suggest that the air flow rates that I used were inappropriate. Because of the constraints on inducing wild wrens to sing in a metabolic chamber while in temporary captivity, the chamber had to be relatively large. Although the air flow rates that I used to estimate metabolism during singing could be considered low for so large a chamber, they represent a compromise between flow rates that are high enough for accurate estimates of oxygen consumption yet low enough to prevent "windy" conditions that could change a wren's singing behavior and thermal conductance. Although there is a chance that chamber air was not mixing completely in the time span of typical singing bouts, inadequate mixing would most likely lead to underestimates of oxygen consumption rather than to overestimates. Misleadingly high measurements of oxygen consumption would occur only if the wrens were breathing directly into the oxygen analyzer while singing (or into the outlet of air going to the oxygen analyzer), and this certainly was not the case. Most wrens sang while they were perched in the lower sections of the chamber, whereas the air outlet was in an upper corner away from the perches. Thus, inadequate mixing of air would have resulted in conservative estimates of energy expenditure rather than in overestimates as the authors suggest.

Data analysis.—Gaunt et al. call for clarifications and additional information not contained in my original paper. In response to their request, and toward stimulating further dialog and research on this topic, I provide additional information below.

Given the problem of small sample sizes for my comparisons of singing rates and oxygen consumption, all conclusions about higher oxygen consumption resulting from faster singing rates must remain tentative, as I stated in the original paper. Gaunt et al.'s efforts to make further conclusions about singing rate are not valid because by removing an outlying data point or by examining trends within individuals, the data are weakened beyond usefulness.

However, it is interesting that the same overall trend is apparent when partially controlling for the confounding effects of variation in accompanying non-singing behavior. Energy consumption again appears to increase ($r_s = 0.68$, $n = 9$, $P = 0.053$) with singing rate (see Fig. 1). In this comparison, energy consumption is measured as oxygen consumption during singing compared with oxygen consumption measured during non-singing activity just before singing. Prior and simultaneous behaviors included hopping quickly between perches and perching quietly, with behavior patterns too unpredictable and inconsistent to distinguish consistently between hopping and nonhopping bouts. Thus, oxygen consumption of activity prior to a singing bout was calculated with the same method used in standard metabolism measurements under the assumption that activity level overall had reached an equilibrium state.

I did not include this analysis in my original paper because little is known about how energy expenditures of different behavior patterns add up when behavior patterns are performed simultaneously (Goldstein 1988). I include it now only because Gaunt et al. specifically asked for such information. Because wild Carolina Wrens typically perform other activities while singing (pers. obs.), it was valid to measure oxygen consumption during singing regardless of other concurrent behaviors. Clearly, however, the influence of other behaviors on measurements of singing costs would be an important factor to consider in future research.

Gaunt et al. question my use of standard metabolic rates (SMR) for comparison with oxygen consumption rates during singing. As I stated at the end of the Results section, a SMR of each wren was measured at approximately the same ambient temperature as was used in the singing trials. With such a comparison, differences in ambient temperature could inflate the apparent cost of singing if SMR were lower than expected. Low SMR might occur if measurements of SMR were made in the thermal neutral zone and thus at warmer temperatures than those used for singing bouts. I controlled for this problem as carefully as possible given the constraints of a large metabolic chamber housed in room air. Ambient temperatures for 7 of 10 SMR measurements were equal to or lower than those for corresponding singing bouts. In the other three cases, temperatures during SMR measurements were no more than 2°C higher than those of their respective singing bouts. Thus, my comparisons of oxygen consumption during singing with SMR were unlikely to be inflated by temperature differences. Using this comparison with SMR helps control for the problem of individual variation in overall oxygen consumption and therefore allows data from several individuals to be analyzed together.

In the Discussion of my original paper, I also compared oxygen consumption during singing with basal metabolic rate (BMR). Although differences in individuals probably make my prior SMR comparisons more valid, the metabolic costs of various behavior patterns usually are reported in the literature as multiples of BMR (e.g. Goldstein 1988). Thus, for my comparisons with reported energetic costs of other behaviors (e.g. flight, perching, preening, etc.), the use of BMR was a better choice.

What are the costs?—Any discussion of energy expenditure during singing must employ the word "cost" and related words carefully. Gaunt et al. state that "Although singing may be energetically expensive relative to perching, eating, or preening . . . it may be *cheap* in comparison with alternative behaviors that might serve the same purpose" (emphasis mine). This type of statement implies that the only cost to consider, be it "cheap" or "expensive," is the energy expenditure necessary to perform the behavior. However, behaviors such as display may have much more important (and possibly much more expensive) costs, e.g. increasing the displayer's vulnerability to predators or expending time that might be spent foraging. In all explorations of the "cost" of a specific behavior, scientists should be careful to specify the currency of the cost and not forget the other dimensions of the lives of their study animals. Even in the title of their commentary ("Is Singing Costly?"), Gaunt et al. imply that only one type of cost (energy expenditure) for singing is important.

A measurable energy expenditure.—My research on oxygen consumption by singing Carolina Wrens is one of the first studies of this type on passerine birds. My estimates have been constrained by the needs of wild birds temporarily held in captivity. If anything, my measurements probably represent low values compared with wild wrens because of the low flow rates I used and the lack of full singing postures exhibited by captive birds. Clearly, singing has a measurable energetic cost, but its importance remains to be determined. Future studies must address overall costs of singing (of which energy expenditure is just one part) to avoid the unsubstantiated assumption that "singing is cheap."

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