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Received 18 September 1995, accepted 13 November 1995.

The Auk 113(3):718–721, 1996

Is Singing Costly?

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In an interesting paper testing for the energetic cost of singing in a passerine bird (Carolina Wren, *Thryothorus ludovicianus*), Eberhardt (1994) concluded that singing in passerines is a costly activity that "accounts for 9.4 to 24.7% of the total energy budget." She attributed this cost to sexual selection for expensive displays. We find this paper disturbing at several levels. In order of increasing specificity, these are: (1) the author's interpretations exceed the limits of her data and are linked to questionable theoretical considerations; (2) the data, even if correct, are subject to alternative interpretations; and (3) the method used to obtain and analyze the physiological data is questionable.

Theoretical problems.—Eberhardt (1994:124) stated, "Theories of sexual selection predict that mate choice

will lead to the evolution of costly displays that indicate the health or condition of displayers." True, some theories do make such predictions (Zahavi 1987), and some elaborate signals may reasonably be attributed to such tactics (e.g. long tails in weaver finches; Andersson 1992). However, theories of sexual selection predict only that costly displays are one means of advertising fitness, if this is in fact truly an issue. That sexual selection does appear to employ costly displays in some species does not suggest that this condition is universal. Further, reliable signals need not be costly (Maynard Smith 1994), and "liars" may be penalized by various means. When and where might we expect costliness to be appropriate?

It is generally supposed that organisms expend considerable energy to enhance reproductive success and that energy so expended may be parceled to various activities, each of which contributes to total success (Cody 1966). If the energy available for reproduction is limited, then parceling approaches a zero-sum game.

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This relationship allows us to predict that costly pre-nuptial displays likely decrease a male's efforts in parental behavior. Therefore, costly displays are most likely to occur in polygynous species where, as Eberhardt noted, it may be driven by sexual selection.

What is meant by costly? The assessment of cost supposes a basis for comparison. Although singing may be energetically expensive relative to perching, eating, or preening (but evidently is not so expensive in chickens; Chappell et al. 1995), it may be cheap in comparison with alternative behaviors that might serve the same purpose. Advertising displays should eliminate the need to patrol boundaries. Thus, such displays must alert receivers to the presence of the sender, even if the sender is unaware of the receiver's location or presence. The signal, therefore, should intercept all possible routes of approach. Many birds, especially small passerines, defend three-dimensional territories, and their advertising displays should be adapted to saturate a volume (bounded by a surface), not a planar surface (bounded by a line). Chemical displays do occupy volumes but are difficult to confine to a particular volume. Visual displays require uninterrupted lines of sight not available in many forested or semiopen environments. 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. Like visual displays, acoustic displays also can be directed, if need be (Wiley and Richards 1982).

Eberhardt cited Lambrechts and Dhondt (1988) as "evidence" that bird song can be limited by energetics. In fact, Lambrechts and Dhondt's hypothesis that large repertoires decrease exhaustion of syringeal muscles is unsupported by muscle physiology in general and is contrary to what is known of syringeal muscle physiology (Suthers and Hector 1985, Lalatta-Costerbosa et al. 1990) and avian vocal mechanics in particular (Gaunt and Gaunt 1985). Readily available information should have signaled caution in this area. Animals have evolved many mechanisms for the maintenance of long-term, repetitive activities, else such behaviors as long-distance migration or breathing would not be possible. Such mechanisms include ordered recruitment of motor units, proliferation of aerobic fiber types, and elaboration of the circulatory supply. The syringeal muscles in Oilbirds (*Steatornis caripensis*; Suthers and Hector 1985) and several species of anatids (Lalatta-Costerbosa et al. 1990) are reported to have many mitochondria and other features similar to the pectoralis muscles in long-distance fliers (syringeal muscles of chickens and several oscines also appear to be adapted for endurance; A. S. Gaunt pers. obs.). Some syringeal muscles are necessarily active during normal ventilation to prevent the syrinx from collapsing into a configuration similar to that used for sound production; denervation of these muscles can result in collapse of the syrinx and asphyx-

iation (Nottebohm 1971). Further, the muscles in the avian vocal system most susceptible to exhaustion are the ventilatory muscles of the body wall, which are responsible for producing the high air pressures used to drive avian vocal systems, whereas syringeal muscles need only adjust the configuration of the syrinx (Gaunt 1988). Prolonged singing and the emission of continuous sound require special adaptations of the ventilatory musculature that permit reversal of flow (i.e. mini-breaths; Calder 1970, Hartley and Suthers 1989).

Alternative explanations.—On the basis of literature indicating that singing increases when birds are provisioned with supplemental food, Eberhardt judged that this supplemental fuel energized singing activity. However, foraging activity itself may involve such potentially costly activities as rapid locomotion among sites, pursuit of prey, manipulation of a substrate, and manipulation of food items. Supplemental food (or captivity) can free a bird from many activities associated with feeding. The bird, thus, is provided with "leisure time" in which to sing.

Eberhardt reviewed several studies indicating that, because singing is a costly activity, singing rate declines with decreasing ambient temperature. We interpret this to mean that, because of high avian metabolic rates, lowering temperatures inflict a high energy cost in thermoregulatory activities. Hence, a cold bird is preoccupied trying to maintain body temperature and, therefore, stops singing. The smaller the bird the higher the mass-specific metabolic rate (Marschall and Prininger 1991). Given that maintenance of corporal temperature is energetically expensive, the bird now engages in this crucial activity at the expense of all nonvital activities. In our view, the bird ceases singing not because singing requires a lot of energy, but because it consumes some energy, however trifling, that is best used otherwise.

Data acquisition and analysis.—Because most singing bouts did not last long enough for the oxygen content of the chamber to reach equilibrium during a bout of singing, Eberhardt used the method of Bartholomew et al. (1981) to calculate instantaneous rate of oxygen consumption. However, the characteristics of her measurement system, most particularly the large ratio of chamber volume to flow rate, render questionable the accurate measurement of brief, episodic changes in rates of oxygen consumption (Frappell et al. 1989). Complete mixing of chamber air is essential if short-term changes are to be calculated accurately by the method used; and both large over- and underestimations of the instantaneous rate of oxygen consumption are possible if this condition is not met. Yet, Eberhardt provided no assurance that adequate mixing was achieved.

The critical airflow rate for the chamber (McNab 1988) is not a relevant concept, especially if one is attempting to measure instantaneous, as opposed to steady-state, rates. The Depocas and Hart (1957) equa-

tion (used by McNab 1988) is not used to calculate instantaneous rates of oxygen consumption and is appropriate for only steady-state situations. Even if an animal consumes oxygen at a constant rate, inadequate mixing or flushing of a metabolic chamber due to low flow rate can give an erroneously high or low rate of oxygen consumption over a limited time period in air sampled as it leaves the chamber. Whether the value is high or low depends on what fraction of the animal's exhaled breath mixes with what fraction of the total volume of air in the chamber. Over longer time periods (still assuming a constant rate of oxygen consumption), a steady-state equilibrium will be achieved, and a true rate of oxygen consumption can be measured. The time necessary to reach a steady state depends upon the combination of flow rate with chamber size and on the mixing characteristics within the chamber. The fact that identical resting metabolic rates ("a stable, constant rate"; Eberhardt 1994:125) were reached in both experimental chambers is not relevant to assessing the validity of short-term, peak metabolic rates determined during singing bouts by using Bartholomew et al.'s (1981) method of calculating instantaneous rates.

The data presented could have been clarified by including other kinds of information presumably available to the author. What was the duty factor (percent time actually spent singing) for each bird? We realize that measurement periods were limited, but even knowing the time from the beginning of the first to the end of the last song in each case would help. Assuming that the rates of oxygen consumption in Eberhardt's table 1 are mean values for the number of bouts given, how contiguous in time were the bouts? The rates of singing varied. Did the length of time spent singing correlate, negatively or positively, with the singing rate? What was the temporal relationship between singing and recorded changes in rate of oxygen consumption, and how was it established? Within individuals, except for one value for one bird (Eberhardt 1994:fig. 2), factorial oxygen consumption appears to be negatively correlated, or not correlated at all, with singing rate. A faster rate did not have a higher cost! Was there a relationship between singing rate and previous singing activity?

At what ambient temperature were the singing measurements made? Did the temperatures differ between individuals? If so, how might this difference have affected the factorial scope? An increase in oxygen consumption over basal cannot be attributed solely to singing if ambient temperature was below the lower critical temperature. Sometimes Eberhardt discussed factorial scope as a function of standard metabolism (presumably accounting in some way for temperature effects), but in the Discussion, she reported increases as multiples of basal metabolic rate and, thereby, implicated singing alone as responsible for the increase. Further, if one wishes to generate a range of costs for singing in wrens, each individual

wren's maximum rate of oxygen consumption should be related to its own basal metabolic rate, not to a mean basal metabolic rate for the species.

How much activity accompanied singing, and how was its cost differentiated from the cost of singing per se? The method used to establish the temporal concordance between the time of singing and oxygen consumption record (which has some characteristic time lag related to the flow rate) is very important if there was any other activity before, after, or during singing. In constructing an energy budget based upon the measurements she made, the author should have used daytime standard metabolic rates, not nighttime rates, in partitioning costs.

Concluding remarks.—We are especially concerned that investigators not intimate with this subject may inappropriately generalize Eberhardt's findings. Eberhardt's data are in stark contrast to those from new sources (Chappell et al. 1995, Horn et al. 1995). Especially puzzling is the fact that a passerine species, which might be presumed to have an efficient syrinx (Gaunt 1983), should be so much less competent than a rooster, which is reported to be remarkably inefficient in its ability to convert mechanical energy to sound (Brackenbury 1977). It is, of course, possible that Carolina Wrens are guilty of conspicuous consumption for whatever purpose.

Perhaps Eberhardt is correct and will be vindicated by subsequent data, just as Calder (1970), who also exceeded his data in the formulation of the mini-breath hypothesis, was vindicated by experiments with improved techniques (Hartley and Suthers 1989). Until such data are available, we find her findings intriguing, but we remain skeptical.

Acknowledgments.—We thank Joseph Williams for discussions concerning the physiological aspects of this critique. Comments of Marlene Zuk and two anonymous reviewers considerably improved the presentation.

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Received 9 January 1995, Accepted 2 March 1995.

The Auk 113(3):721-723, 1996

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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