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Oxygen consumption during crowing by roosters: talk is cheap

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Abstract. The energetic cost of signalling may be important in maintaining the honesty of the signal, yet it is rarely measured directly. Oxygen consumption during crowing by roosters, *Gallus gallus domesticus*, was measured in a closed-circuit indirect calorimeter. Although there was a positive relationship between crowing and O_2 consumption, roosters consumed only 0·005 ml/g/h for each vocalization. Thus at the average crowing rate, O_2 consumption rate would be 15% above standing, which is less than the cost of low-level activities such as feeding, drinking and preening, and over 10 times less than the maximum sustainable metabolic rate. These results contrast with previous reports of high energy consumption during calling in insects and frogs, which approach or exceed maximal levels. Other costs, such as predation and social retaliation, are probably more important than energetic costs in maintaining crowing as an honest signal.

Much recent research in animal communication has focused on whether animal signals convey honest information. Most models suggest that signals are honest because they are costly to produce (Enquist 1985; Grafen 1990a, b; Godfray 1991). If a signal is expensive to produce, senders should signal only if they can afford the cost. In the case of aggressive or mate attraction signals, for example, senders should bear a cost in proportion to their fighting abilities or potential quality as a mate (Enquist 1985; Grafen 1990a, b). In the case of begging signals, the trade-off between the costs of begging and the benefits of being fed should result in offspring giving signals whose costs are in proportion to the offspring's needs (Godfray 1991).

Costs of producing signals may include attraction of predators (e.g. Ryan et al. 1982; Yasukawa 1989), retaliation by conspecifics (Enquist 1985; Møller 1987), and energetic costs (Ryan 1988). Energetic costs may be the most widespread cost to signal production, because any activity expends energy. Also, many display behaviour patterns, especially those used in contests and in mate attraction, are elaborate and appear to be strenuous.

Most direct measurements of the energetic costs of displays have been taken on insects and frogs, which show 5–30-fold increases in oxygen consumption during calling (Ryan 1988). Direct measurements on endotherms are scarce and inconclusive. Using doubly labelled water, metabolic rate during sexual displays in sage grouse, *Centrocercus urophasianus*, was estimated as 13–17 times basal rate, but this figure includes the cost of travelling to and from the display site (Vehrencamp et al. 1989). Telemetric monitoring of heart rate during calling in one black duck, *Anas rubripes*, suggested costs comparable to low-level activities such as preening and drinking (Wooley & Owen 1978), whereas heart rate during singing in a small sample of blackbirds, *Turdus merula*, showed a wide range of patterns (Diehl 1992). A laboratory study of oxygen consumption during singing in one adult and three immature Carolina wrens, *Thryothorus ludovicianus*, showed consumption levels five times above standard metabolism (Eberhardt 1994). However, the contribution of other activities to this value was not specified (Nagy 1987; Goldstein 1988). The same study showed a correlation between singing rate and oxygen consumption, but this analysis did not control for individual differences.

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Most additional evidence for energetic costs in endotherms is indirect. For example, red deer, *Cervus elaphus*, lose weight during the rut, which involves constant roaring and little foraging (Clutton-Brock et al. 1982). Great tits, *Parus major*, sing progressively shorter and slower songs during rapid bursts of singing, whereas in several species of songbird singing rate is increased by provisioned food (Lambrechts 1992). Although such results suggest that vocal signalling is energetically limited, alternative explanations are also likely. For example, food provisioning may increase the value of a territory and hence the profitability of territory defence.

Given the importance of birds and mammals in the study of animal communication, direct measurements of the energetic cost of signalling in these groups are clearly needed. The purpose of our study was to measure oxygen consumption during crowing by roosters, *Gallus gallus domesticus.* Roosters are well suited to such a study because they readily vocalize in respiration chambers. Also, the act of crowing is mechanically inefficient; only 1·6% of the power of the air passing through the syrinx is translated into sound energy (Brackenbury 1977). We thus predicted that crowing was energetically expensive, particularly compared to the songs of passerine birds, which appear to produce sound more efficiently (Brackenbury 1979). Finally, crowing is a reliable signal of male dominance (Leonard & Horn 1995), making it reasonable to expect that high energetic costs might be one way to maintain such a signalling system.

METHODS

Subjects

Subjects were 19 white leghorn roosters, 26–28 weeks old and weighing 1930 ± 30 g ($\bar{X} \pm$ SE). Males were reared with females from hatch to 18 weeks in floor pens (measuring 3·65 × 5·10 m), with ad libitum water and food. At 19 weeks we transferred them to standard single-male cages (measuring 30 × 30 × 40 cm), again with food and water available ad libitum. All subjects received the same feed mix. While they were housed in the floor pens, we observed the birds daily and weighed them every 2 weeks. Thus they were relatively accustomed to being handled and disturbed.

Apparatus

We measured metabolism in a closed-circuit indirect calorimeter (Fig. 1), modelled after those previously used on poultry (Waring & Brown 1965; Miller et al. 1981). We placed a rooster in a sealed 45-litre chamber in which pressure was equalized by allowing oxygen to enter the chamber, in this case from the fresh air around the chamber rather than from a pure oxygen source as in the previous studies. In a conditioning circuit, air from the chamber was pumped at 2·4 l/min through two 600-ml cylinders of soda lime (to absorb CO_2) and anhydrous calcium sulphate (to absorb water), through a copper coil immersed in a cold water bath, and back into the chamber. We measured oxygen concentration by drawing air at 100 ml/min from the portion of the chamber nearest the subject's beak through a 115-ml column of anhydrous calcium sulphate and then a Mocon model LF-700D oxygen analyser, which measured oxygen concentration to 0·1%, with a response time of 5 s, by means of a zirconium fuel cell. We multiplied changes in oxygen concentration by 1·2095 (the O_2 concentration of fresh air) to account for the fresh air leaking into the chamber, and converted O_2 volumes to standard temperature and pressure. The total effective volume of the chamber and associated circuits was 47 litres.

Procedure

Metabolic rate may vary considerably among different individuals and ambient conditions, so we conducted two 30-min trials under the same conditions on the same bird, and expressed crowing rate, activity level and O_2 consumption as the absolute difference between the trial with the most crowing and the trial with the least. We conducted tests in the room in which the males were housed, between 1000 and 1600 hours, at 23·5 ± 0·41°C. Before each trial, we placed the subject in the chamber with the lid ajar for a 15-min adaptation to the apparatus. We then closed the chamber and noted all activities (see below), including the number of vocalizations, for 30 min. We then opened the lid for 15 min, after which time we conducted another trial with the same individual. Subjects had ad libitum access to food and water before but not during their time in the chamber.

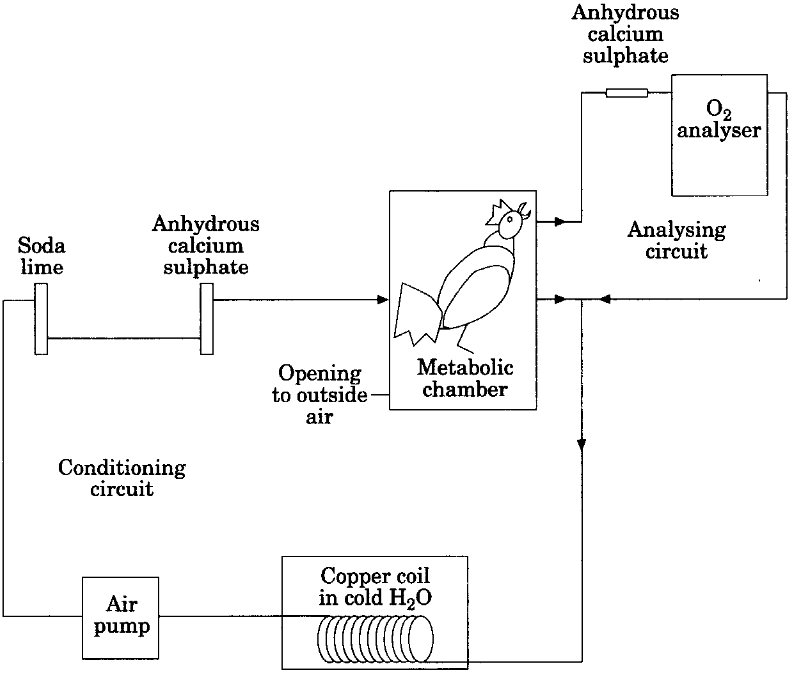

Figure 1. Closed-circuit calorimeter used to measure oxygen consumption during crowing. Arrows show direction of flow of pumped air.

Analysis

We defined the amount of crowing as the number of single acts of crowing, not as the number of crowing bouts or time spent crowing. Activity besides crowing was expressed as the number of 30-s intervals in which the subject moved. This usually consisted of small head movements (present in 82% of 30-s intervals; $N=2480$), although preening, stepping and turning around were seen in 2% of all intervals. Of the 19 males tested, nine crowed in both trials, four crowed in only one trial, and six did not crow in either trial. We used the latter two sets of males ($N=10$) to estimate resting metabolic rate, using trials in which males did not crow, or, if they did not crow in either trial, using only the second trial (to allow as much time as possible for adaptation to the apparatus). All subjects were standing throughout.

RESULTS AND DISCUSSION

The difference in crowing between trials was significantly correlated with an increase in oxygen consumption ($r^2=0{\cdot}48$, $df=12$, $P=0{\cdot}009$; Fig. 2). Oxygen consumption also increased with an increase in activity ($r^2=0{\cdot}32$, $df=12$, $P=0{\cdot}04$), but crowing was not significantly related to activity ($r^2=0{\cdot}23$, $df=12$, $P=0{\cdot}44$), so the relationship

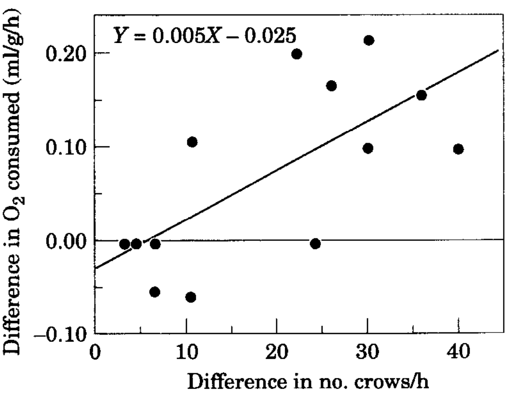

Figure 2. Oxygen consumption rate relative to crow rate for 13 roosters. Two 30-min trials were conducted on each male, and the change in O_2 concentration over the trial in which a male crowed least was subtracted from that in which it crowed the most. This change was compared to the difference in the number of crows between trials.

between oxygen consumption and crowing was not merely a result of increased activity. Controlling for activity levels did not increase the variance explained by crowing ($r^2=0{\cdot}46$ for residuals of relationship with activity versus $r^2=0{\cdot}48$ for original data). The slope of the relationship between change in crowing and change in oxygen consumption (Fig. 2) shows that each act of crowing is associated with an increase in oxygen consumption of 0·005 ml/g/h. Given the mean crowing rate (± SE; 30 ± 3 acts of crowing/h, $N=13$ males), and the mean resting metabolic rate of males that did not crow (1·02 ± 0·037 ml/g/h, $N=10$), O_2 consumption would be raised by only 15% (0·15 ml/g/h) by crowing at the average rate. This rate is comparable to the cost of low-level activities such as feeding, drinking and preening, which in hens raise metabolic rate by 20–28% above resting (MacLeod & Jewitt 1985).

Dominant males crow about 200–250 times per day, whereas subordinate males crow significantly less or not at all (Salomon et al. 1966; Mench & Ottinger 1991; Leonard & Horn 1995). For caged males, whose activity is necessarily restricted, crowing at the rate of a dominant would account for less than 10% of the daily energy expenditure, assuming that the crowing would use 1–1·25 ml O_2/g/day and assuming a daily energy expenditure of 437–469 kJ/kg$^{0{\cdot}75}$/day; i.e. about 13 ml O_2/g/day (Freeman 1983). This figure is based on the daily energy budgets that are available in the literature for males of various layer breeds. The true figure for wild males, for example red junglefowl, *G. g. spadiceus*, would be much less, because wild birds would spend more energy on other activities, especially locomotion (Nagy 1987).

The energetic cost of crowing should be well within the energetic capabilities of any individual. Males running on a treadmill can reach a maximum consumption rate of 12 times the resting metabolic rate (Brackenbury & Avery 1980). If conditions were severe, for example because food was scarce or in very cold temperatures, some individuals might crow less to save energy. Severe conditions do not explain the large differences in crowing rate associated with dominance status, however, because these persist even in captive studies when food is not limited (Leonard & Horn 1995).

The weight of males with higher than expected oxygen consumption during crowing (i.e. above the line in Fig. 2) was not significantly different from that of males with lower oxygen consumption (i.e. below the line in Fig. 2; higher: 1920 ± 101 g, $N=7$; lower: 1980 ± 44 g, $N=6$, $t=-0{\cdot}51$, $P=0{\cdot}619$). This analysis is post hoc and therefore preliminary, but it does suggest that the incremental cost of crowing did not vary according to the condition of the male.

Thus energetic costs do not seem to be high enough to account for the relationship between crowing and dominance, and therefore for the maintenance of crowing as an honest signal of status. Other costs may be more important in maintaining this signalling system. First, high crowing rates might attract predators. Although there is almost no direct evidence for predation costs to bird vocalizations (cf. Yasukawa 1989), roosters do fall silent in the presence of potential predators (Collias & Collias 1967). Second, crowing may carry a social cost. When subordinate roosters crow, they are often immediately attacked by more dominant individuals (Leonard & Horn 1995). Third, time spent vocalizing may take time away from foraging (Hutchinson et al. 1993; but see Mace 1989). Finally, crowing may honestly signal a male's health. Among the first symptoms of most poultry diseases are irregularities in respiration, such as gasping and wheezing (North 1984). Diseased males might not be able to produce loud and clear crowing, even before their energy budgets are affected.

Our results clearly cast doubt on the assumption that vocal displays are energetically costly to endotherms. We might expect singing in many songbirds to be relatively cheap as well, because they vocalize at a higher rate but apparently with greater mechanical efficiency than roosters (Brackenbury 1979). Proper tests of models of animal signalling will require additional measurements of the energetic costs of vocalization in particular, and display behaviour in general.

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