Energy cost of an avian vocal display: crowing in red junglefowl

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Displays are important components of social behaviour and are potential targets for sexual selection. Females may prefer males with particular behavioural repertoires, and several models of sexual selection suggest that males with elaborate or prolonged courtship displays could be indicating their quality to females (Kirkpatrick & Ryan 1991; Maynard Smith 1991). Males may also use displays in intra-sexual contests involving alternation of behaviour patterns (e.g. roaring in red deer; Clutton-Brock & Albon 1979). Implicit in these concepts is the assumption that displays are costly: opponents and potential mates could assess male quality by observing displays because males of high quality should be better able to support display costs. In fact, some evolutionary models suggest that no signal can contain useful information unless it entails some cost to the signaller (Grafen 1990). This cost is partially metabolic and displays are often assumed to substantially impact energy budgets (e.g. Vehrencamp et al. 1989). However, there have been few attempts to directly measure the energy cost of displays, and these are largely confined to courtship songs of insects and frogs. Calling in these animals is indeed rather expensive: metabolic power output during signalling can be many-fold greater than resting metabolism (e.g. McNally & Young 1981; Prestwich & Walker 1981; Prestwich et al. 1989).

Despite intensive study of the display behaviour of birds and mammals, we are aware of only one direct metabolic measurement of their display costs. Eberhardt (1994) reported a substantial cost of singing (three to nine times basal metabolism) in Carolina wrens, *Thryothorus ludovicianus*. Here we examine the energetics of a familiar avian display: crowing in red junglefowl, *Gallus gallus*. Male junglefowl crow during both male–male and male–female interactions (Collias 1987; Zuk et al. 1990). The 1·5–2-s duration display is loud (~95 dB in the closely related domestic chicken *G. g. domesticus*; Brackenbury 1978), stereotyped, and appears to require intense muscular effort.

The consistency of this signal, and the fact tha is usually not accompanied by other locomo activity, make it amenable to investigation energy cost.

We obtained birds from a captive colony l under semi-natural conditions. Males used the study were at least 8 months old and experience interacting with other junglefowl. used open-flow respirometry to measure ene metabolism of single birds. The metabolic ch ber was a 60-litre Plexiglas box supplied with air at rates of 10–12 standard litres/min. Oxy content of excurrent air (dried and scrubbe CO_2) was measured with an Applied Electroch istry S-3A analyser connected to a computer sampled every 2·5 s. We computed 'instantane oxygen consumption ($\dot{V}O_2$; ml O_2/min) to incr resolution of rapid changes in $\dot{V}O_2$ (Bartholo et al. 1981). The system resolved response very brief events, such as episodes of preenin scratching lasting less than 2 s. Measurem took place between 0900 and 1600 hours in r light at thermoneutral temperatures (27–30°C

Most birds crowed spontaneously, ofter bouts of 3–20 crows at inter-call interval 15–120 s. Although we did not measure it dire crowing in the chamber appeared identica duration, amplitude, and accompanying m ments to that of uncaged males. We placed m ers in data files whenever birds crowed, and noted preening, pecking and postural change

Our starting hypothesis was that crowin correlated with elevated $\dot{V}O_2$. If crowing is ex sive, single crows should be associated with t sient increases in $\dot{V}O_2$. If the cost of crowin small, single crows might not be resolvable bouts should be associated with increases in proportional to the frequency and numbe crows in the bout. There was no effect of ei single crows or bouts of crowing on $\dot{V}O_2$ (Fig We compared $\dot{V}O_2$ during bouts (at least t crows with inter-call intervals <60 s) with the immediately before and after bouts. In most c
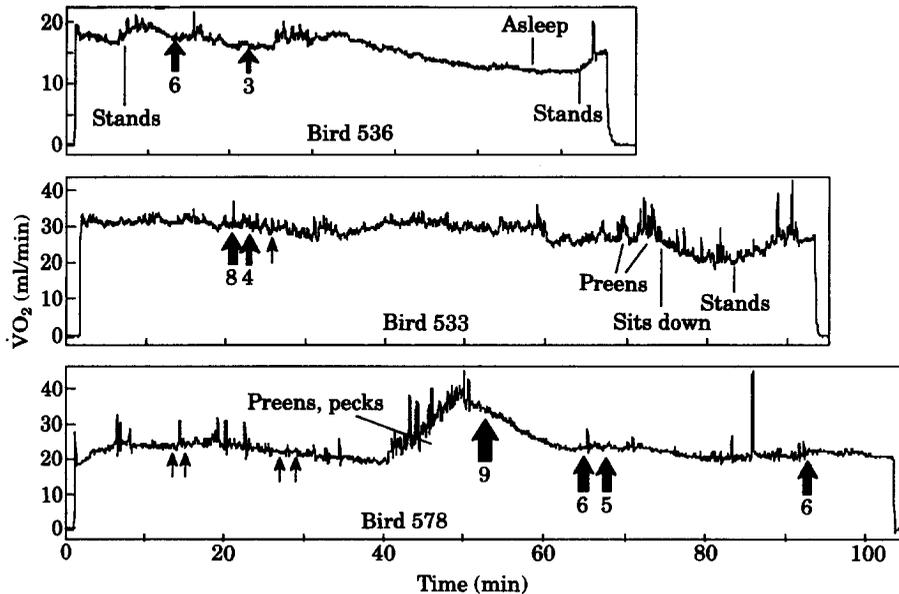
Figure 1. Rates of oxygen consumption ($\dot{V}O_2$) of male red junglefowl during calling and other activities. Single crows are indicated with small arrows; bouts of crowing are indicated by large arrows (numbers indicate the number of crows in each bout). For reference, basal metabolic rates are 10–12 ml O_2/min.

the duration of 'before' and 'after' measurement periods equalled bout duration. When necessary, we used shorter 'before' and 'after' periods to avoid overlap with other crows. The $\dot{V}O_2$ during 20 bouts ($7\cdot4 \pm 3\cdot4$ crows/bout; bout duration 197 ± 120 s; inter-call interval $26\cdot9 \pm 8\cdot5$ s; 12 birds) did not differ from the mean $\dot{V}O_2$ before and after bouts (sign test: $z=0\cdot22$, $P=0\cdot82$).

These results suggest that the energy cost of crowing is very small, which is surprising because crowing subjectively appears to require considerable effort. Crowing costs are less than noise levels in recorded metabolic rates (from short-term metabolic fluctuations, uneven mixing and electrical noise). To estimate the maximum crowing cost our system would fail to detect, we used the standard deviation (SD) of $\dot{V}O_2$ during periods when birds were inactive and metabolism was stable. The SD (21 periods; 11 birds) averaged $0\cdot55$ ml O_2/min. Accordingly, our detection threshold for crowing cost is 4–5% of basal metabolism (unpublished data) and about $2\cdot5\%$ of the average $\dot{V}O_2$ during our measurements. It is worth noting that energy costs of many routine activities (e.g. preening, scratching, or simply standing up) are much higher than the cost of crowing.

Brackenbury (1978) calculated that peak power delivery associated with air movements during crowing in $3\cdot3$ kg chickens was $2\cdot25$ W (2000 times as large as during normal respiration), and pointed out that actual energy requirements are higher because of muscular inefficiency. Are his estimates consistent with our results? To convert Brackenbury's data to $\dot{V}O_2$, we assumed power output was constant during crows, scaled air volume to the mass of male red junglefowl ($1\cdot4$ kg), and used a power conversion efficiency (muscle power to air movement) of 30%. At call durations of $1\cdot5$ s and inter-call intervals of $26\cdot9$ s energy use is $10\cdot6$ J/min, equivalent to $0\cdot53$ ml O_2/min and quite similar to our detection threshold.

The low cost of crowing in red junglefowl contrasts sharply with high signalling costs in insects, frogs and Carolina wrens. Several factors could account for the difference between junglefowl, frogs and insects. First, the 'duty cycle' (the fraction of time spent vocalizing) during calling bouts was 5–6% in junglefowl, while many insects and frogs call nearly continuously for long periods (e.g. Prestwich & Walker 1981; Prestwich et al. 1989). Second, because red junglefowl are endotherms, their resting metabolic rate, upon which

crowing costs are superimposed, is comparatively very large. For example, a call with an energy cost equal to our detection threshold would be equivalent to ~25% of the resting metabolism of a 1·4 kg ectotherm (instead of 2·5% of resting metabolism in junglefowl). Finally, junglefowl are 100 to more than 1000 times larger than most frogs and insects, but their calls are only ~10 to ~100-fold louder (Forrest 1991). The larger mass/acoustic power ratio in junglefowl increases the background metabolism against which crowing costs must be measured and should be compared.

Cost differences between junglefowl and Carolina wren calls are more difficult to interpret, but some of the above arguments are relevant. These wrens are 70-fold smaller than junglefowl and sing at higher rates (8–30 songs/min; Eberhardt 1994), although duty cycles per se were not reported. Eberhardt did not report resolution limits for her system, but the very large ratio of chamber volume to flow rate she used (13·7 litres; 0·5–0·7 litres/min) is not conducive to accurate measurement of brief metabolic events, even if an instantaneous conversion is used.

The small cost of crowing in red junglefowl is interesting in light of Zuk et al.'s (1990) finding that females pay little attention to this display when selecting mates. In these experiments, pairs of males presented to a female often differed markedly in the number of crows performed during the observation period, but there was no evidence that this influenced female preferences.

To summarize, the crowing of red junglefowl has no detectable energetic significance even though it is an extremely obvious signal. This counter-intuitive result should serve as a caution to researchers making assumptions about the effects of energy costs on the evolution of displays, and about using display rate as an estimate of energy expenditure and hence of physiological health and vigour, at least for vertebrate endotherms. Display vocalizations in some birds and mammals, particularly small species with loud calls and high duty cycles, may have a substantial energy cost, as is frequently claimed. However, our results suggest that such assertions should be treated with scepticism unless they are validated with careful metabolic measurements. Energetic considerations aside, other costs of displays, such as increased vulnerability to predators and parasites, reduction of time available for oth activities, etc., remain as important evolutiona factors.

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