

CORRESPONDENCE


The metabolic cost of whistling is low but measurable in dolphins

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We read ‘Whistling is metabolically cheap for communicating bottlenose dolphins (*Tursiops truncatus*)’ by Pedersen et al. (2020) and were concerned to see how our results (Noren et al., 2013; Holt et al., 2015) were presented. This was especially surprising, given our previous feedback to the authors (see acknowledgements, Pedersen et al., 2020). Although Pedersen et al. claim their work disproves our findings, their methods were not designed to accurately measure the low metabolic cost (MC) of whistle production. In fact, the differing conclusions are explained by differences in methods and interpretation of the findings.

Pedersen et al. (2020) ‘reject the hypothesis that whistling is costly for bottlenose dolphins.’ This ‘hypothesis’ is attributed to our publications. To be clear, we reported that the average metabolic rate (MR) for whistling dolphins is 1.2× resting metabolic rate (RMR) and concluded that ‘there is a measurable, though relatively small, metabolic cost to dolphins producing sounds, including whistles’ (Noren et al., 2013). Comparatively, MRs of whistling dolphins fall between those of sitting humans watching television (1.0× RMR) and typing (1.5× RMR, Ainsworth et al., 1993) and are comparable to MRs of stationary, sound producing birds (see Noren et al., 2013; Pedersen et al., 2020). We verified through video analysis that movement by whistling dolphins was minimal (Holt et al., 2015).

The experimental design in Pedersen et al. (2020) makes it challenging to detect the low MC of whistles. Noren et al. (2013) and Holt et al. (2015) measured dolphins whistling at the water surface via flow-through respirometry with a metabolic hood. Respiration rates (RRs) of whistling dolphins did not differ from RRs pre- and post-sound production (Noren et al., 2013). Importantly, we used statistical analyses to determine when MR returned to RMR during 10 min recovery periods (Noren et al., 2013). In contrast, Pedersen et al. used breath-by-breath respirometry with a pneumotachometer to measure dolphins following apneustic periods. The accuracy of breath-by-breath respirometry is impacted by dolphins’ very high respiratory flows and short breath durations (Fahlman et al., 2015), which would make measuring the low MC of whistling difficult. Pedersen et al. did not evaluate changes in MR during recovery periods. This is critical, as dolphin MRs typically recover within <5 min following sound production (ranges, means±s.d.: 0–5.8 min, 3.2±1.9 min, unpublished data from Holt et al., 2015; 2.8–6.7 min, 4.9±1.2 min, Noren et al., 2013).

Although Pedersen et al. were unable to directly measure whistling MRs in submerged dolphins, they conducted a large number of trials, randomized over the experimental period. Using this experimental design, the most direct method to estimate the MC of whistling, while accounting for MR variability, is to compare post-apnea MC across trial types. Although Pedersen et al. reported no difference, the average MC of apnea+whistling was 1.15× the average MC of apnea during control trials and was nearly significantly different ($P=0.06$), indicating whistling MC similar to those reported in our studies.

Our studies compared daily matched RMR and sound production MR to account for daily MR fluctuations that could mask the MC of sound production (Noren et al., 2013; Holt et al., 2015). Pedersen et al. estimated whistling MR using assumptions that critically affected their results. First, oxygen consumption measured during 2 min pre-apnea is assumed to represent RMR. This is problematic because this short time period may not accurately estimate RMR (see Compher et al., 2006). Second, data from the entire 5 min recovery period are included. This is problematic because the small elevation in MR from whistling is present during a fraction of this period. Consequently, the average MR masks the MC of whistling. Thus, it is not surprising that the estimated whistling MR (1.04× RMR, Pedersen et al., 2020) is lower than our measured value (1.2× RMR, Noren et al., 2013; Holt et al., 2015). Interestingly, this 4% increase in MR is still greater than the maximum theoretical predicted increase (0.5–1%, Jensen et al., 2012). Consistent with our studies (Noren et al., 2013; Holt et al., 2015), Pedersen et al. showed highly variable metabolic responses in whistling dolphins. Some individuals had noticeably higher whistling MCs (Table 3, Fig. 4, Pedersen et al., 2020). Given these results, it would be informative to know how oxygen consumption changed over the recovery period and how these changes varied by individual, trial, and sound energy levels. This would be relatively easy to provide.

Comparisons between the metabolic cost of whistling and squawking, as presented in Pedersen et al., are erroneous. Squawking dolphins can have higher MRs (1.5× RMR, Holt et al., 2015) than whistling dolphins. This may be related to potentially differing metabolic demands associated with using different muscles to produce the distinct sounds (Ridgway et al., 1980). Pedersen et al. used data for squawking dolphins from our studies to estimate dolphin sound production efficiency (Fig. 6). Holt et al. (2015) clearly state that calculating sound production efficiency from our data is inappropriate, given a multitude of reasons, which were ignored. Consequently, Fig. 6 from Pedersen et al. is misleading and some readers may mistakenly assume that the value presented is for whistling dolphins.

Finally, three studies report that the MC of clicking, whistling, and squawking increases with sound duration and/or energy levels in dolphins (Noren et al., 2013, 2017; Holt et al., 2015). Yet, Pedersen et al. use results of their study, which aimed to measure sound production efficiency, rather than MCs of vocal modification, to conclude that there is no cost associated with the Lombard effect.

In summary, contrary to conclusions in Pedersen et al., their results align with ours. They were unable to detect the small MC of whistling in dolphins because of the use of less-sensitive respirometry methods and data modeling. Their conclusion that 1.2× RMR is a high MC is invalid, given that MRs of most sound producing dolphins fall within the large range of dolphin RMRs (Fahlman et al., 2015, 2019) and the greater MC of other activities in free-ranging cetaceans (Noren et al., 2013).

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Response to: The metabolic cost of whistling is low but measurable in dolphins

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Costs of sound production have been investigated only sparsely in cetaceans, despite recent efforts to understand how increasing anthropogenic noise affects these animals that rely extensively on sound for communication and foraging. Theoretical estimates suggest that metabolic costs of whistling for bottlenose dolphins should be <0.54% of resting metabolic rate (RMR) (Jensen et al., 2012), whereas empirical studies of a single whistling dolphin surprisingly claimed that sound production costs were around 20% of RMR (Holt et al., 2015; Noren et al., 2013). Addressing this discrepancy, we found that costs of whistling were significantly less than 20% RMR and not statistically different from theoretical estimates (Pedersen et al., 2020). In their correspondence, Noren et al., 2020 argue that they did not claim whistling was ‘costly’ and questioned aspects of our methods, and we address these points here.

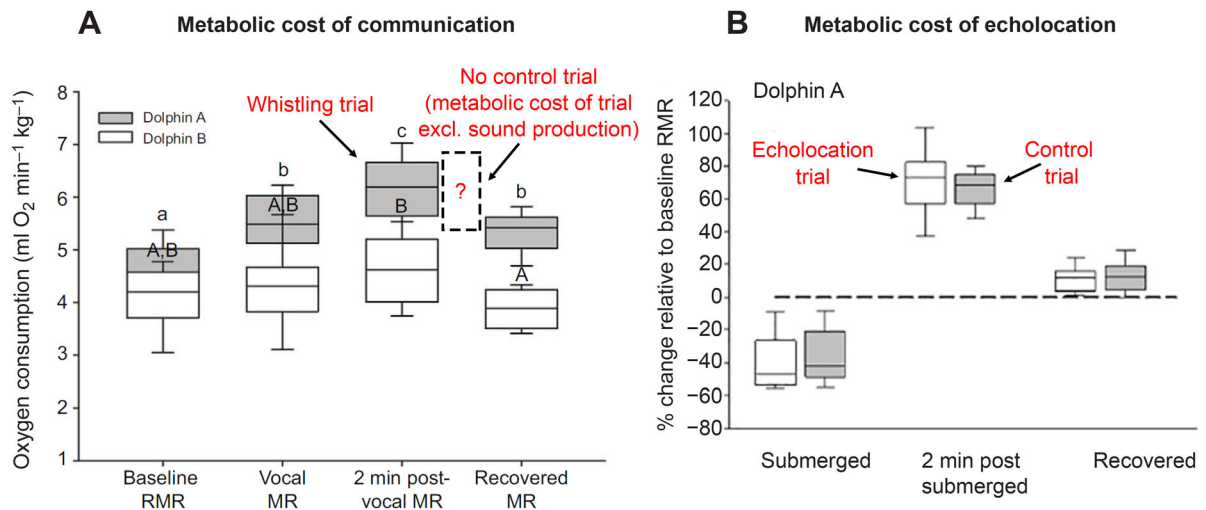
The ‘costly sound production’ hypothesis

Sound production efficiency is the ratio between emitted acoustic energy and the metabolic energy consumed to generate sound. Mammals, frogs, and birds produce sound with an efficiency of ~0.4–3.0% (Pedersen et al., 2020). Acoustic efficiency has not been measured for marine mammals; consequently, we assumed an efficiency of 1% to estimate a theoretical metabolic cost of 1.7 J per whistle (Jensen et al., 2012). Noren and colleagues (2013) stated that ‘a theoretical approach to determine the metabolic costs of

sound production in dolphins may be inaccurate’ and that the discrepancy is due to ‘the incorporation of incorrect variables (e.g. efficiency factor)’. Holt et al., (2015) estimated that the trial with most acoustic energy contained ‘approximately 0.08 J of [acoustic] energy’, and incurred a metabolic cost of 82,067 J, suggesting an ‘extremely low calculated efficiency factor range (less than 0.1%)’. While the authors report an estimated efficiency resembling that of other species, their numbers yield an extremely low efficiency of 0.0001%. This discrepancy is independent of their acoustic measurements – even if trained animals had vocalized at peak output levels of wild animals (~1 J emitted acoustic energy per trial), efficiency would have been no greater than ~0.001%. Thus, while the authors deny labelling dolphin communication ‘costly’, their studies directly indicate that dolphins are 3–4 orders of magnitude less efficient at producing sound than any other species studied.

Was there in fact any evidence of costly sound production?

Noren et al. (2013) found a significant cost of whistling but a non-significant cost of producing a burst-pulse squawk and concluded that ‘there is a measurable, though relatively small, metabolic cost to dolphins producing sound’. Subsequently, Holt et al. (2015) found a significant correlation between metabolic costs and acoustic output for the squawking but not the whistling dolphin, concluding that ‘vocal performance



Are control trials needed? (Oberweger and Goller, 2001)

NO	Communication is costly (Noren et al., 2013, Holt et al., 2015)	Echolocation is costly (wrong conclusion)
YES	Noren et al., 2013, Holt et al., 2015 inconclusive (Pedersen et al., 2020: Whistling is NOT costly)	Echolocation is cheap (Noren et al., 2017)

Fig. 1. Silent 'control' trials are needed to demonstrate metabolic costs were caused by sound production rather than other factors that might elevate metabolic rate. (A) Data from Noren et al. (2013) with the lack of control trial indicated for a whistling trial. (B) Data from Noren et al. (2017) for an echolocation trial with a control trial highlighted. Bottom panel illustrates how study conclusions depend on silent control trials and shows how missing control trials would have led to wrong conclusions about cost of echolocation.

affects metabolic rate'. To reach that conclusion, 9/29 trials (squawking) and 3/27 trials (whistling) were discarded because the metabolic rate after sound production was lower than RMR. Such data omissions and subjective statistical interpretations weakens support of their conclusions that theory is wrong by 3–4 orders of magnitude.

Improved methods for quantifying small changes in metabolism

Noren et al. (2020) argue that our experimental design was unsuitable for detecting the low costs of whistling. Pedersen et al. (2020) measured breath-by-breath respirometry before and after a breath-holding period to track the rate of oxygen consumption. In contrast, Noren and colleagues (2013) used a traditional flow-through respirometry system where each breath was diluted in a respirometry dome with a system lag time of 36.5 s. If this lag time is the system time constant, it would take ~ 1.5 min to evaluate changes in metabolic rate (Fahlman et al., 2008). This could explain why their estimated metabolic rates took on average 3.2–4.9 min to return to baseline, compared with an average 1.2 min recovery after apnea when using a breath-by-breath system (Fahlman et al., 2019). Our finer temporal resolution facilitates shorter measurement periods, which in turn may improve results as it is often difficult to prevent animal movement during longer inactive periods. This might explain why vocal or post-vocal metabolic rates were higher than RMR >50% of the time for one animal (Noren et al., 2013) and in 11% and 31% of trials subsequently (Holt et al., 2015). The authors also claimed that the breath-by-breath system cannot detect the 'small' differences in metabolic cost because of the high respiratory flow and short breath durations of dolphins. As expiratory durations were on average 50% longer than required to accurately detect the O_2 uptake, this is not an issue (Fahlman et al., 2015). In fact, this method

accurately measures low metabolic costs (control measurements within 0.5% of RMR) and so is likely more suitable for quantifying small changes in metabolism than dome respirometry.

Attributing metabolic costs to sound production

Past studies attempting to assess the metabolic cost of sound production may have included confounding effects unrelated to sound production, such as changes in movement, posture, or even cognitive demands or stress associated with trained tasks. To account for such effects, it is necessary to include silent 'control' trials, which are identical but without sound production (Fig. 1; see also Oberweger and Goller, 2001). Noren et al. (2017) demonstrate the importance of this – by comparing metabolic costs during echolocation trials to metabolic costs during silent control trials, they found no measurable costs of echolocation; however, without a control trial, echolocation would have appeared costly. Such silent control trials are missing from the Noren et al. (2013) and Holt et al. (2015) studies, and thus, in repeating a problem known in the bird literature for >10 years, these studies make it impossible to attribute changes in energetic demands unequivocally to sound production.

In conclusion, Pedersen et al. (2020) provide results that agree with theory and show that dolphins, like any other animal relying on sound for communication and foraging, have evolved efficient ways of producing sound. Thus, metabolic costs of increasing vocal outputs in elevated anthropogenic noise, such as through the Lombard response (Kragh et al., 2019), are predicted to be low.

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