

RESEARCH ARTICLE

The metabolic cost of communicative sound production in bottlenose dolphins (*Tursiops truncatus*)

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SUMMARY

Bottlenose dolphins (*Tursiops truncatus*) produce various communicative sounds that are important for social behavior, maintaining group cohesion and coordinating foraging. For example, whistle production increases during disturbances, such as separations of mother–calf pairs and vessel approaches. It is clear that acoustic communication is important to the survival of these marine mammals, yet the metabolic cost of producing whistles and other social sounds and the energetic consequences of modifying these sounds in response to both natural and anthropogenic disturbance are unknown. We used flow-through respirometry to determine whether the metabolic cost of sound production could be quantified in two captive dolphins producing social sounds (whistles and squawks). On average, we found that metabolic rates measured during 2 min periods of sound production were 1.2 times resting values. Up to 7 min were required for metabolism to return to resting values following vocal periods. The total metabolic cost (over resting values) of the 2 min vocal period plus the required recovery period (163.3 to 2995.9 ml O₂ or 3279.6 to 60,166.7 J) varied by individual as well as by mean duration of sounds produced within the vocal period. Observed variation in received cumulative sound energy levels of vocalizations was not related to total metabolic costs. Furthermore, our empirical findings did not agree with previous theoretical estimates of the metabolic cost of whistles. This study provides the first empirical data on the metabolic cost of sound production in dolphins, which can be used to estimate metabolic costs of vocal responses to environmental perturbations in wild dolphins.

Key words: marine mammal, metabolic cost, metabolism, oxygen consumption, whistle.

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INTRODUCTION

Like other animals, many marine mammals produce sounds during biologically important activities such as socializing, foraging and reproduction. In bottlenose dolphins, for example, signature whistles provide identity information (Caldwell and Caldwell, 1965; Sayigh et al., 1999), and are used to maintain group cohesion (Janik and Slater, 1998; Cook et al., 2004). These whistles are produced when groups of dolphins meet and join at sea (Quick and Janik, 2012), when individuals are separated from their group (Janik and Slater, 1998) and when mother–calf pairs are separated (Smolker et al., 1993). Furthermore, whistles may serve as indicators of stress as their parameters change in response to a variety of stressors (Esch et al., 2009). For example, signature whistles are produced more frequently during vessel approaches (Buckstaff, 2004). Thus, increased ship traffic in recent years, including marine mammal focused boat excursions, may increase the rate at which bottlenose dolphins produce signature whistles. Because these animals are dependent on acoustic signals for survival, and the rate of whistle production may increase as ship traffic increases in the environment, it is important to understand the metabolic cost associated with producing basic acoustic signals, such as signature whistles. An understanding of the energetic costs of sound production may also provide a means of quantifying fitness tradeoffs associated with call production (Gillooly and Ophir, 2010; Ophir et al., 2010).

The energetic cost of sound production has been well studied in insects, amphibians and birds (for reviews, see Ophir et al., 2010; Stoddard and Salazar, 2011). Like most signals, acoustic signals are produced at an energetic cost to the signaler; the magnitude of these costs varies across species (Ophir et al., 2010). Few studies, however, have been conducted on mammals, and these are limited to bat and human subjects. The findings suggest that the metabolic cost of sound production in mammals is relatively low. For example, echolocating bats that are producing one pulse per second while hanging at rest have a small, but measureable, increase in metabolism relative to resting values [1.4× silent resting values (Speakman et al., 1989)]. During flight, the metabolic cost of echolocation is negligible because of the overall high metabolic cost of flying (Speakman and Racey, 1991). Russell et al. (Russell et al., 1998) found no difference in oxygen consumption between quiet breathing and speaking at a comfortable sound pressure level in humans. There are no empirical data on the cost of sound production in any marine mammal. Odontocetes (toothed whales) produce sounds in an anatomically different way compared with other mammals [*via* the nasal complex as opposed to the larynx (Cranford et al., 2011)] and have the added constraint of a limited oxygen supply while diving. These differences in anatomy and ecology could influence the metabolic cost of sound production. Indeed, the metabolic cost of sound production varies greatly within and across taxa (Ophir et al., 2010; Stoddard and Salazar, 2011), and these differences may

be related to such factors as resting metabolic rate, body mass, body temperature and the relative size of the sound-producing muscles that are active during calling (Ophir et al., 2010).

In this study we measured oxygen consumption in two captive bottlenose dolphins during rest and while vocalizing at relatively low to moderate sound levels to determine whether the metabolic cost of sound production could be quantified. This information is crucial to understanding the daily energy budget of dolphins and will also provide data to assess whether changes in sound production parameters, which can occur during periods of disturbance, can affect daily energy budgets, and hence daily energetic requirements, of odontocetes.

MATERIALS AND METHODS

Subjects

The metabolic cost of sound production was measured in two adult male Atlantic bottlenose dolphins [*Tursiops truncatus* (Montagu 1821)] maintained at Long Marine Laboratory in Santa Cruz, California. The dolphins, Dolphin A and Dolphin B, were 31 and 25 years old, respectively, and had been housed together at this facility in two outdoor pools (100,000 and 42,000 gallon) for 16 years when this study commenced. The water temperature was controlled and did not fluctuate more than 2°C over the study period (average temperature: 20.0±0.6°C). Animals were maintained on a diet of herring and capelin (herring: ~256 g per fish, 1.96 kcal g⁻¹; capelin: ~23 g per fish, 1.01 kcal g⁻¹; T.M.W. and T. Kendall, unpublished data) and supplemented with a daily multivitamin (Seatabs, Mazuri, Richmond, IN, USA).

Both dolphins had been trained for over 10 years, using operant conditioning techniques and positive reinforcement, to station under a metabolic hood for collection of oxygen consumption data. The dolphins were trained for an additional period of 6 months to produce sounds on command while stationed under the hood prior to data collection for the present study. The sounds of free-ranging Atlantic bottlenose dolphins have been described as clicks, whistles, buzzes, quacks and pops (Jacobs et al., 1993). The trained sounds of the captive dolphins were representative of those found in wild, free-ranging populations. All behaviors were performed voluntarily with animals free to leave the experimental apparatus or stop vocalizing at any point throughout the trials. All procedures were approved by the University of California, Santa Cruz Institutional Animal Care and Use Committee and conducted under National Marine Fisheries Service permit no. 13602 to T.M.W.

Experimental design

Experimental trials were conducted on dolphins following an overnight fast. Only one experimental trial was conducted per dolphin per day, and subjects were run separately. Each experimental trial consisted of three phases: (1) initial baseline period, (2) vocal period and (3) recovery period. During the baseline period, the dolphin remained still at the water surface under the metabolic hood for 10 min to allow measurement of resting metabolic rate (RMR). During the vocal period, the dolphin produced sound at the water surface in two consecutive 1 min bouts that were separated by 15–20 s of silence. The 15–20 s break was incorporated into the protocol for behavioral reasons, and no metabolic recovery was believed to occur during this time. During the recovery period, the dolphin again remained still at the water surface for another period of rest to measure recovery (at least 10 min, or until % O₂ returned to approximately resting values). Dolphins were rewarded with herring and capelin only after completing the entire experimental trial.

The total duration of the baseline, vocal and recovery periods was recorded for each experimental trial. Respirations were also recorded during each of the three periods. A total of 14 trials were conducted per dolphin. One trial per dolphin was excluded from the analysis due to behavioral reasons (e.g. failure to consistently vocalize or remain stationary while under the metabolic hood). As a result, a total of 13 trials per dolphin were included in the analysis.

Oxygen consumption data collection and analysis

Oxygen consumption (\dot{V}_{O_2}) was measured using flow-through respirometry methods for quiescent dolphins resting and producing sounds at the water surface. Air was drawn into the hood at a flow rate of 300 l min⁻¹ to ensure that oxygen content in the hood remained above 20%. Water and CO₂ from subsamples of excurrent air from the hood were absorbed using Drierite (W. A. Hammond Drierite Co., Xenia, OH, USA) and Sodasorb (Chemetron, St Louis, MO, USA), respectively, prior to entering the oxygen analyzer. The percentage of oxygen in the sample line was monitored continuously (TurboFox Complete Field System, Sable Systems International, Las Vegas, NV, USA) and recorded by a laptop computer every second during experimental trials. The oxygen analyzer was calibrated daily using dry ambient air (20.95% O₂). The system was checked for leaks and the lag time was determined using the N₂ dilution method (Fedak et al., 1981) twice weekly.

Markers for the start and end of all components of the experiment (e.g. baseline, vocal and recovery periods) were entered into the computer and plotted on the % O₂ time series during the experiments. These markers were adjusted for the system's lag time prior to analysis. \dot{V}_{O_2} for baseline, vocal and recovery periods was calculated from the % O₂ data by respirometry software (Expedata Data Acquisition & Analysis Program, Sable Systems International) that incorporated eqn 4b from Withers (Withers, 1977).

For all experimental trials, RMRs were calculated by averaging \dot{V}_{O_2} during the most level 5 min (determined by the 'level' function in Expedata) of the last 8 min of the baseline resting period. Metabolic rates (MRs) during vocal periods were calculated by averaging \dot{V}_{O_2} from the beginning of the first vocal bout to the end of the second vocal bout. Average MRs during the first 2 min of the recovery period (hereafter referred to as the '2 min post vocal period') were also calculated to demonstrate that \dot{V}_{O_2} often remained elevated after vocal bouts ceased. Recovered MRs were calculated by averaging \dot{V}_{O_2} during the most level 5 min (determined by the 'level' function in Expedata) of the recovery period.

The total metabolic cost of sound production (sound production plus recovery costs, excluding baseline resting cost) and total recovery time were calculated by first integrating oxygen consumption against time and then fitting two parallel linear regressions to the integrated data. The first linear regression was fitted to the 5 min of level baseline data (the baseline RMR) and the second was fitted to the post-vocal period. For this analysis, the post-vocal period included the period from the end of the trial to 10 min previous, during which time the dolphin was presumed to reach the recovery state. The difference in the intercepts between each regression is equal to the total cost above the resting rate established in the baseline period. Once the total metabolic cost had reached 95% of the total costs for the vocal plus recovery period, the animal was considered to have reached a recovered state and the elapsed time between the start of the vocal bout and the recovered time is reported as the recovery time.

Acoustic data collection and analysis

Sounds produced during all trial components were acoustically monitored in real-time and recorded using calibrated equipment to

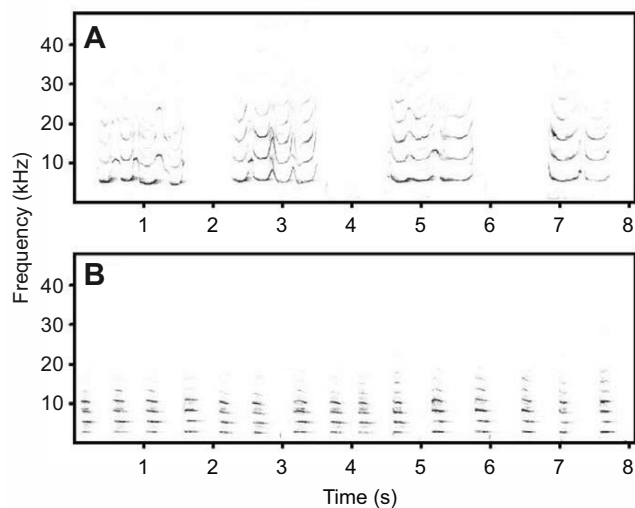


Fig. 1. Spectrograms showing 8 s examples of sounds produced during the vocal period of each trial by (A) Dolphin A (whistles) and (B) Dolphin B (squawks).

quantify vocal performance. The recording equipment included a Reson TC-4033 hydrophone (nominal sensitivity: -203 dB re. 1 V/ μ Pa, ± 3 dB from 0.02 to 94 kHz; Reson, Goleta, CA, USA). Calibration was periodically checked with a pistonphone connected to a custom adaptor (42AA with RA78; GRAS Sound & Vibration, Holte, Denmark). The hydrophone was connected through a bandpass filter and amplified using a Reson VP 2000 preamplifier, digitized at a sampling rate of 96 kHz (16 bit resolution) using a MOTU Traveler (MOTU, Cambridge, MA, USA) and then recorded and monitored in real-time using a customized version of Ishmael 1.0 (Mellinger, 2001).

All sounds produced during the vocal period of each trial were analyzed in Avisoft SASLab Pro (v. 5.1.17; Avisoft Bioacoustics, Berlin, Germany). Sound files were digitally high-pass filtered (128 taps, Hamming window, filter setting: 1.5 and 2.0 kHz for Dolphin B and Dolphin A, respectively) to remove extraneous low-frequency sounds. Each vocalization was windowed using the automatic parameter measurement feature and numerically labeled. Vocalization measurements included start and end time, duration, interval (from start of the preceding to start of current vocalization), received acoustic pressure (μ Pa) and received acoustic energy (Pa^2s). Measurements in the frequency domain (e.g. peak frequency at start and end, maximum peak frequency) were also made but varied little within and between trials. The total number of vocalizations, mean duration, mean received acoustic pressure and received cumulative sound energy were calculated for the vocal period of each trial. The mean sound pressure level (SPL; dB re. 1 μ Pa) and cumulative sound

energy level (SEL; dB re. 1 $\mu\text{Pa}^2\text{s}$) were then converted from linear scales. Recordings were also inspected to assess whether dolphins produced sounds during the baseline and recovery periods. Because low-level clicks and whistles were occasionally produced during these periods in some trials we investigated whether the production of these sounds affected the metabolic results. Unfortunately, received levels of clicks could not be measured because of the restricted bandwidth of the acoustic recording system. Thus, we assessed whether the number of click trains and whistles/squawks produced during the baseline and recovery periods were related to recovery duration and total metabolic cost.

Statistical analysis

Respiration and oxygen consumption data were compared across trial components using one-way repeated-measures ANOVA or an equivalent ANOVA on ranks when tests for normality and/or equal variance failed. When results were significant, pairwise comparisons were made using the Holm–Sidak method (ANOVA) or a Tukey's test (ANOVA on ranks). Linear regression analyses were used to assess whether the number of click trains and whistles/squawks produced during the baseline and recovery periods were significantly related to recovery duration and total metabolic cost. A P -value of 0.05 was considered to be the critical statistical level of significance. All means are presented ± 1 s.d.

RESULTS

Each dolphin produced the same sound type during his vocal period, but the sounds produced were qualitatively different between the two dolphins. Specifically, Dolphin A produced a whistle (trained from capturing his signature whistle) while Dolphin B produced what we describe as a pulsed squawk or squeak-like sound (see spectrograms, Fig. 1). Dolphin B's pulsed sound is similar to the quack sounds described by Jacobs et al. (Jacobs et al., 1993).

A total of 13 trials per dolphin were included in the analysis. Acoustic parameters of vocal periods are presented in Table 1. Little variation in the frequency domain was observed among vocalizations within a dolphin (Fig. 1). Whistles/squawks produced during the baseline and recovery periods of trials were much lower in received cumulative SEL, even in the worst cases, compared with those produced during the vocal period (Table 1). For example, the highest SEL during the baseline period for Dolphin A was 116.2 dB re. 1 $\mu\text{Pa}^2\text{s}$ due to the production of four whistles, and for Dolphin B was 100.1 dB re. 1 $\mu\text{Pa}^2\text{s}$ due to the production of 17 squawks. The number of sounds produced during baseline and recovery periods was not significantly related to total recovery duration or total metabolic cost (all $P > 0.05$). Note that the received sound levels reported here were measured from a hydrophone in the test pool to compare vocalization performance among trials. Source levels could not be measured because sounds were produced under a reverberant hood at the air–water

Table 1. Summary of acoustic parameters during vocal periods

Dolphin	No. of trials	Sound type	No. of sounds produced	Sound duration (s)	Interval between start of each sound (s)	Received SPL (dB re. 1 μ Pa)	Received cumulative SEL (dB re. 1 $\mu\text{Pa}^2\text{s}$)
A	13	Whistle	63.3 ± 7.2	1.08 ± 0.26	1.91 ± 0.20	127.6 ± 3.5	147.5 ± 3.7
B	13	Squawk	242.2 ± 42.7	0.167 ± 0.037	0.488 ± 0.108	115.4 ± 1.9	132.6 ± 2.5

Vocal periods consisted of one dolphin producing sound in two consecutive 1 min bouts that were separated by 15 – 20 s of silence.

SEL, sound energy level; SPL, sound pressure level.

Means are presented ± 1 s.d.

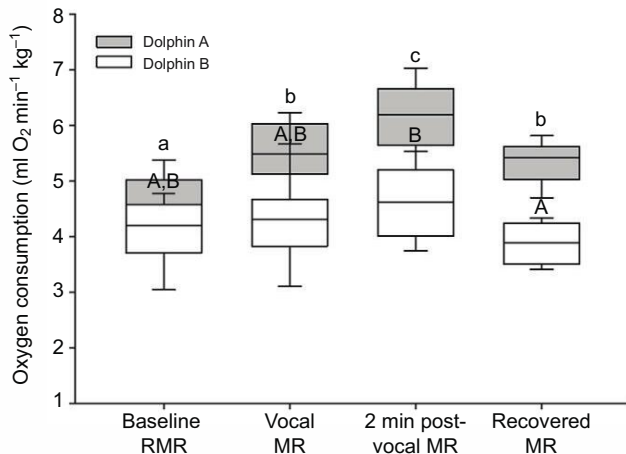


Fig. 2. Oxygen consumption ($\text{ml O}_2 \text{min}^{-1} \text{kg}^{-1}$) measured during components of 13 experimental trials. Data from Dolphin A and Dolphin B are represented by gray and white box plots, respectively. For each box plot, the boundary of the box closest to zero indicates the 25th percentile, the solid line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Error bars above and below the box indicate the 90th and 10th percentiles, respectively. Distinct letters (Dolphin A: lowercase, Dolphin B: uppercase) designate significantly different ($P < 0.05$) oxygen consumption values.

interface and received levels are likely underestimates of entirely water-propagated sounds.

The % O_2 data showed that dolphins incur a measurable metabolic cost during the production of both types of sounds and that recovery to baseline levels occurs gradually after the vocalization periods cease. The increase in MR ($\text{ml O}_2 \text{min}^{-1} \text{kg}^{-1}$) during the vocal period over RMR varied by individual dolphin and by trial (Fig. 2). The mean percent increase over RMR was 21.5 ± 7.7 and $5.9 \pm 17.7\%$ for Dolphin A and Dolphin B, respectively. The low mean percent increase in MR for Dolphin B was due to MRs during vocalizations being lower than RMRs for some trials. Thus, it is possible that this dolphin was not in a true rested state during the baseline period of these trials. These trials were not removed from the statistical analysis, though, because there were no obvious behavioral reasons to exclude them. However, if these trials are removed from this particular calculation, then the mean percent increase in MR over RMR increases to $17.5 \pm 16.2\%$ for Dolphin B.

For both dolphins, there was a statistically significant difference in MR (Dolphin A: $P < 0.001$, Dolphin B: $P = 0.023$) across the four analysis components (baseline RMR, vocal MR, 2 min post-vocal MR and recovered MR). Pairwise comparisons demonstrate that the relative cost of producing sound and the recovery pattern after sound production for the two dolphins differed slightly. For Dolphin A, vocal MRs ($5.5 \pm 0.6 \text{ ml O}_2 \text{min}^{-1} \text{kg}^{-1}$) were significantly greater ($P < 0.001$) than baseline RMRs ($4.6 \pm 0.5 \text{ ml O}_2 \text{min}^{-1} \text{kg}^{-1}$), and MRs often did not return to baseline levels during the recovery period (Fig. 2). Interestingly, 2 min post-vocal MRs ($6.1 \pm 0.7 \text{ ml O}_2 \text{min}^{-1} \text{kg}^{-1}$) were not only significantly greater ($P < 0.001$) than baseline RMRs, but were also significantly greater ($P = 0.006$) than vocal MRs and recovered MRs ($5.3 \pm 0.4 \text{ ml O}_2 \text{min}^{-1} \text{kg}^{-1}$, $P < 0.001$; Fig. 2). Even though the trend was similar for Dolphin B, the only statistically significant result was that 2 min post-vocal MRs ($4.6 \pm 0.7 \text{ ml O}_2 \text{min}^{-1} \text{kg}^{-1}$) were greater than recovered MRs ($3.9 \pm 0.4 \text{ ml O}_2 \text{min}^{-1} \text{kg}^{-1}$, $P = 0.021$;

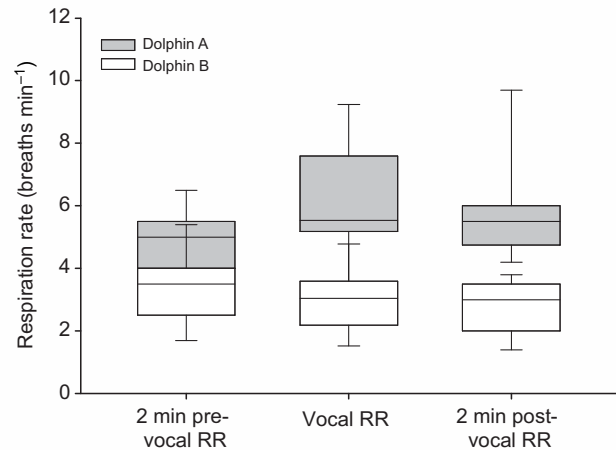


Fig. 3. Respiration rate (breaths min^{-1}) recorded during components of 13 experimental trials. Data from Dolphin A and Dolphin B are represented by gray and white box plots, respectively. For each box plot, the boundary of the box closest to zero indicates the 25th percentile, the solid line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Error bars above and below the box indicate the 90th and 10th percentiles, respectively. There were no significant differences in respiration rate values across the three trial components for either dolphin.

Fig. 2). Although MRs varied significantly across the different components, respiration rates recorded for 2 min immediately prior to the vocal period, during the 2 min vocal period and for 2 min immediately following the vocal period did not differ significantly for either dolphin (Dolphin A: $P = 0.314$; Dolphin B: $P = 0.219$; Fig. 3).

The total oxygen consumed during the vocal period plus the required recovery (over resting values) and the duration required for recovery were distinctly different for the two dolphins. The metabolic cost of Dolphin A's vocal period plus recovery ranged from 754.5 to 2995.9 ml O_2 (mean: $2009.1 \pm 624.6 \text{ ml O}_2$) above resting values, and 2.8 to 6.7 min (mean: $4.9 \pm 1.2 \text{ min}$) were required for oxygen consumption to return to resting values following the completion of the vocal period. For Dolphin B, the metabolic cost of the vocal period plus recovery ranged from 163.3 to 1834.0 ml O_2 (mean: $885.8 \pm 762.9 \text{ ml O}_2$) above resting values, and 1.3 to 7.1 min (mean: $4.9 \pm 2.2 \text{ min}$) were required for oxygen consumption to return to resting values following completion of the vocal period. It is important to note that these results include less than 50% of Dolphin B's trials. This is because trials with elevated oxygen consumption during the baseline period, relative to oxygen consumption during the vocal period, violate a key assumption of the regression analysis.

It is evident that the above results varied widely by individual and by trial within an individual. This is likely related to variability in sound production performance across trials. Indeed, there was a positive linear relationship between mean whistle/squawk duration and the metabolic cost of the vocal period (Fig. 4). This relationship was significant for Dolphin B ($P = 0.043$) but insignificant for Dolphin A ($P = 0.085$). However, it is likely that the relationship is also valid for Dolphin A because the power of the statistical test was low (power = 0.404). Low sample sizes and high variability across samples can result in statistical tests with low power, which increases the probability of accepting a false null hypothesis (Zar, 1996). In contrast, the number of whistles/squawks produced during the vocal period was not linearly related to total metabolic cost of

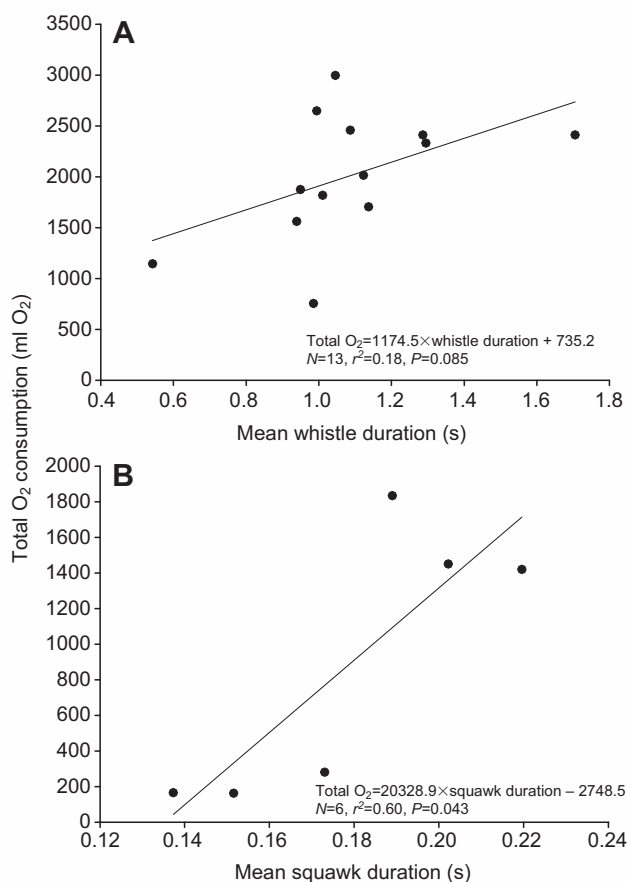


Fig. 4. Total oxygen consumption (ml O₂) over resting values during the vocal and recovery periods combined in relation to the mean duration (s) of (A) Dolphin A's whistles and (B) Dolphin B's squawks. Linear regressions are designated by solid lines, and the equations and statistical results are presented for each plot.

the vocal period (Dolphin A: $P=0.115$, Dolphin B: $P=0.358$). Mean SPL, cumulative SELs, as well as linear versions of these two parameters (i.e. mean acoustic pressure in μPa and cumulative acoustic energy in Pa^2s), were also not linearly related to total metabolic cost of the vocal period (all $P>0.05$).

DISCUSSION

This is the first study to provide empirical data on the metabolic cost of sound production in any marine mammal species. The findings from this study demonstrate that there is a measurable, but variable, energetic cost (163.3 to 2995.9 ml O₂ or 3279.6 to 60,166.7 J) to bottlenose dolphins producing sounds during a 2 min vocal period. Variability in vocal performance influences the metabolic cost of sound production. Specifically, the mean duration of individual whistles/squawks within the vocal period is positively related to the total oxygen consumed during the vocal period and required recovery duration. We also found that respiration rates were similar across the three components of the experimental trial (Fig. 3). Thus, increased oxygen consumption during the vocal period is likely due to increased metabolic demand related to the production of sound, rather than changes in breathing patterns. This metabolic demand is likely related to tissue vibrations that produce the fundamental frequency of dolphin tonal calls (Madsen et al., 2012).

Differences in vocal behavior between the two dolphins revealed some interesting findings. Dolphin A produced relatively longer whistles with higher cumulative SELs and metabolic costs compared with Dolphin B, who produced relatively shorter squawks with lower cumulative SELs and metabolic costs (Table 1, Fig. 2). Oxygen consumption increased with mean duration of the sound produced (Fig. 4), but not SEL, though the range of SEL was restricted. Longer sounds, in general, seem to be more costly to produce, which might be related to sound production mechanisms. For example, whistles require higher nasal air pressure than (much shorter) echolocation clicks in bottlenose dolphins (Cranford et al., 2011). Sustaining higher air pressure levels in the nasal cavity may require more muscular energy, resulting in greater metabolic costs.

Our findings can be compared with results of a previous study that estimated the metabolic cost of dolphins performing whistles *via* theoretical calculations based on acoustic energy (Jensen et al., 2012). These researchers estimated that an adult dolphin would expend 1.7 J per whistle (Jensen et al., 2012). Thus, the estimated cost for 62 whistles (average number of whistles produced during Dolphin A's 2 min vocal period) would be 105.4 J. We empirically found that this metabolic cost actually ranged from 15,152.6 to 60,166.7 J for Dolphin A. Furthermore, we found that variation in the total sound energy produced during the vocal period (measured as cumulative SEL) was not related to variation in metabolic cost in either dolphin. This demonstrates that a theoretical approach to determine the metabolic cost of sound production in dolphins may be inaccurate. This discrepancy is likely related, at least in part, to the incorporation of incorrect variables (e.g. efficiency factor). Thus, until additional information on the physiology and energetics of the dolphin sound production system are available, we caution against using the acoustic energy in the signal to estimate the metabolic cost of producing it.

To put our results in perspective, we can compare the results of the present study with those of studies that empirically measured the metabolic cost of sound production in other adult endothermic vertebrates. Previous studies on bats (Speakman et al., 1989), humans (Russell et al., 1998) and birds (for a review, see Stoddard and Salazar, 2011) measured MRs during sound production and during rest, rather than calculating the total metabolic cost of a vocal bout. MRs of echolocating bats producing one pulse per second while hanging at rest are $1.4 \times \text{RMRs}$ (Speakman et al., 1989). This relative increase in metabolism is similar to what we found for Dolphins A and B (vocal MRs = $1.2 \times \text{RMRs}$) producing an average of 0.5 whistles and two squawks per second, respectively. The only other mammalian study was conducted on humans (Russell et al., 1998). In contrast to the dolphins, which increased their MRs but did not change their respiration rates during moderate levels of sound production, humans did not change MRs but reduced their respiration rates when speaking at comfortable levels (Russell et al., 1998). There are a greater number of studies on birds. For consistency, we only compare studies that measured a state similar to RMR (e.g. standing quietly, pre-song quiet activity) and MRs during sound production by subjects that moved minimally. For several bird species, MRs during sound production range from approximately $\leq 1.1 \times \text{RMR}$ (Oberweger and Goller, 2001; Ward et al., 2003; Oberweger and Goller, 2001; Ward et al., 2004) to $2.3 \times \text{RMR}$ (Jurisevic et al., 1999). On average, we found that MRs during sound production in dolphins was $1.2 \times \text{RMR}$, which is similar to that of many birds, but at the low end of the range. This cost is similar to dolphins swimming at optimal swimming speeds (Williams et al., 1992; Williams et al., 1993; Yazdi et al., 1999). Other activities, such as leaping or performing breaches, produce larger changes in

MRs (Yazdi et al., 1999; D.P.N., unpublished data). Although MRs during sound production in dolphins appear to be low, recovery durations can last up to 7 min following the completion of a 2 min vocal period. No other studies that we are aware of have determined the duration of time required for MRs to return to RMRs following sound production.

The metabolic cost of a 2 min vocal period may not be biologically significant to an individual dolphin (the energetic cost is equivalent to the caloric content of 0.034 to 0.62 individual capelin or 0.0016 to 0.029 individual herring), but the cumulative cost of producing sounds repeatedly throughout the day is important to consider when estimating daily energy expenditure and prey consumption requirements. Furthermore, the total daily energy expenditure related to sound production may vary by the type, source level, duration and repetition rate of the vocalizations. Indeed, we found that total oxygen consumption increased with the mean duration of individual whistles/squawks. Others have found that oxygen consumption in birds increases with song duration (Oberweger and Goller, 2001; Franz and Goller, 2003), call rate (Horn et al., 1995) and sound intensity (Oberweger and Goller, 2001). Thus, changes in vocal behavior have the potential to significantly increase daily energy expenditure. Studies aimed at determining the metabolic cost of modifying acoustic signals will provide additional data required to assess how vocal responses to environmental disturbance affect daily energy expenditure in dolphins. Environmental factors, which are controlled for in laboratory experiments, may also increase the energetic cost of producing sounds in the wild (Ward and Slater, 2005).

In conclusion, we have shown that there is a measurable, though relatively small, metabolic cost to dolphins producing sounds, including whistles, which are important to maintaining social cohesion and for survival. Furthermore, this study demonstrates that metabolic costs of a 2 min vocal period can vary widely, and this variation is due, in part, to vocal performance. Finally, this study provides preliminary data that can be used, in combination with investigations on the acoustic behavior of wild populations, to assess how modified vocal behavior might affect daily energy budgets of dolphins and other odontocetes.

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AUTHOR CONTRIBUTIONS

D.P.N. and M.M.H. conceived the study. D.P.N., M.M.H. and R.C.D. designed and executed the study. D.P.N., M.M.H., R.C.D. and T.M.W. interpreted the findings. D.P.N., M.M.H., R.C.D. and T.M.W. drafted and revised the article.

COMPETING INTERESTS

No competing interests declared.

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