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Respiration Rates in Captive Beluga Whales (*Delphinapterus leucas*): Effects of Season, Sex, Age, and Body Size

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Abstract

Respiration rates can be used as important indices of health and welfare in animal subjects. In the present study, the respiration rates of captive beluga whales (*Delphinapterus leucas*) (N = 55) were found to be influenced by season (winter-spring rates > summer-fall rates), sex (males > females), age (calves > adults), and body size (smaller adults > larger adults). Significant interactions among these terms were also found for season-by-sex and season-by-age. Additionally, the respiration rates of beluga calves gradually declined to the point where they equaled their mothers by 3 y of age, the same age that other cetaceans achieve mature dive physiology.

Key Words: beluga whale, *Delphinapterus leucas*, calf development, body size, seasonal differences, respiration rate, age differences

Introduction

The number of beluga whales (*Delphinapterus leucas*) held in zoos and seaquarium parks has increased dramatically over the past three decades; therefore, there is now an opportunity to accumulate an in-depth profile of physiological processes in this species. There is simultaneously an important need to establish behavioral norms in order to inform management decisions related to the health and welfare of captive subjects. In this context, the present study documents variations in respiration rate in both juvenile and adult beluga whales.

In cetaceans, exhalation/inhalation occurrences are among the most salient and easily observed events from a human's point of view and, therefore, among the most reliably recorded. Respiratory rate can serve as a crude index of metabolic demand in ways that allow comparisons both across and within species (e.g., Osborne & Milsom, 1993; Noren et al., 2012; Rosen & Trites, 2013). For example, Williams & Noren (2009) reported a positive correlation between respiration rate and swimming speed in killer whales (*Orcinus orca*). Similarly, respiration rates can also provide invaluable windows into the internal states of organisms as they cope with changes in external conditions (e.g., changing seasons) and/or endogenous variables (e.g., activity levels associated with breeding) (e.g., Williams & Noren, 2009).

Both across and within taxa, there is a general trend for respiratory rates to be negatively correlated with body size (Kleiber, 1947; Crosfill & Widdicombe, 1961). Compatible with this, it is common for the young of many species to have higher respiratory rates than do the adults (Iliff & Lee, 1952; Mortola & Noworaj, 1985; Gagliardi & Rusconi, 1997). As a consequence, documenting changes in respiration rate during development may reveal the time course over which metabolic processes of the young transition into those characteristic of adulthood.

As a practical matter, the monitoring of respiration rates in captive environments may provide for the early detection of health/welfare problems, often long before more debilitating symptoms become overt. This can be particularly advantageous for very young animals for which caretaker access to subjects is logistically difficult and the need for health monitoring is particularly acute.

Methods

The subjects of this investigation were 55 beluga whales (*Delphinapterus leucas*) (31 adults, 24 calves) held in captivity at Marineland of Canada (Niagara Falls, Ontario). The adults (8 males, 23 females) had all been wild-caught in the Chukchi Sea and were judged by their size (body length > 2 m) to be either adolescent or adult at the time of capture. At the onset of this investigation, all of these wild-caught whales had been at the Marineland facility for no less than 3 y. The calves (9 males, 15 females) had all been born in captivity at Marineland over an 11-y period (2002 to 2013). In nearly all cases, the births had taken place during summer months as is typical for this species (Kleinenberg et al., 1969; Brodie, 1971; Krasnova et al., 2006). The calves ranged from 1 to 877 d old over the course of this study.

The belugas were observed in three different pools that varied in size from 2 to 8 million liters in volume. In all cases, the belugas were housed outdoors, where ambient air temperature varied from as low as -9° C in the winter to as high as 27° C in the summer. Pool water temperature was moderated by mechanical refrigeration and heating and thus varied only between 12° and 18° C. From year to year, the belugas were kept in different social groupings. However, in all cases, calves and their mothers were housed together in groups of animals that included other mother/calf pairs.

In all, observations were made on 357 d over the 11-y study period, with the number of observation days per subject ranging from 3 to 117 (mean = 32.5 d). Observations occurred between 0700 and 0900 h and ranged from 5 to 30 min in length. Information about prior food intake and swimming speed was not recorded. However, the observations of breath rates were nearly always prior to the whales' first feeding period; and at the times of these observations, the whales were unrestrained and characteristically circling slowly.

Observations were made through underwater viewing windows utilizing a focal-animal paradigm. A breath was inferred to have occurred each time a subject rose to the surface momentarily in the anterior-posterior rolling motion that is characteristic of cetaceans. Although cetaceans do sometimes rise to the surface without taking a breath and also sometimes take more than one breath before re-submerging, separate observations taken above the surface confirmed a nearly perfect one-to-one correspondence between the underwater observations taken and visible/audible confirmation of exhalation/inhalation occurrences at the surface. For each subject, its respiration rate on each day was computed as the total number of breaths (surface rolls) divided by the minutes of observation on that day.

Sixty-five percent of the time in which the respiration rate was collected for a calf, the breath occurrences for its mother were also recorded in the same observation period. In those cases, and for a separate analysis, a ratio was computed for each beluga calf as that calf's respiration rate divided by its mother's respiration rate. On the assumption that environmental factors have similar influences on all whales in a given pool (including mother/calf pairs), this ratio allowed developmental trends in the calves to be assessed independent of other influences.

Body weights were not regularly obtained at this facility. Instead, we used a unitless, linear index of relative size among the adult whales. Six different observers independently estimated each whale's body size as a multiple of the smallest whale. The Pearson correlation coefficient among these six observers ranged between 0.92 and 0.95. For each subject, the average of these estimated proportional sizes was then used as an index of body mass.

For the purposes of analysis, each year was divided into meteorological seasons (Winter = December-February, Spring = March-May, Summer = June-August, and Fall = September-November). Each unique combination of whales across years and pools was assigned a different arbitrary value in a categorical variable that was named Calendar Year-Pool Grouping.

The factors influencing respiration rate were analyzed utilizing a Generalized Linear Mixed Model (GLMM) procedure (*SPSS*, Version 19) with Season, Sex, Age, and their two-way interactions as Fixed Effects, and with Calendar Year-Pool Grouping and Subject as Random Effects, thereby accounting for repeated measures. Analysis of the three-way interaction term was omitted because the uneven distribution of subjects/observations across Season, Sex, and Age made it incomplete (*cf.* Quinn & Keough, 2003).

Results

The results of the GLMM analyses on daily respiration rates were as follows:

Main Effects

- *Season* – Respiration rate (breath/min) was significantly influenced by season ($F_{(3, 1,774)} = 6.7$, $p < 0.001$). In general, respiration rates were greater during winter ($\overline{x} = 2.03$, SD = 1.52) and spring ($\overline{x} = 2.28$, SD = 1.32) than during summer ($\overline{x} = 1.01$, SD = 1.30) and fall ($\overline{x} = 1.60$, SD = 0.93) (Figure 1).
- *Sex* – Overall, the respiration rate of males was somewhat higher than that of females, but this did not rise to the level of statistical significance ($F_{(1, 1,785)} = 3.3$, $p = 0.07$) (Table 1).
- *Age* – As a whole, calves had respiration rates that were 40% higher than those of the adults ($F_{(1, 1,785)} = 5.7$, $p = 0.02$) (Table 1).

Interactions

- *Season by Sex* – A significant season by sex interaction ($F_{(3, 1,774)} = 8.9$, $p < 0.001$) reflected the fact that male/female difference was most prominent during summer (male $\overline{x} = 1.69$, SD

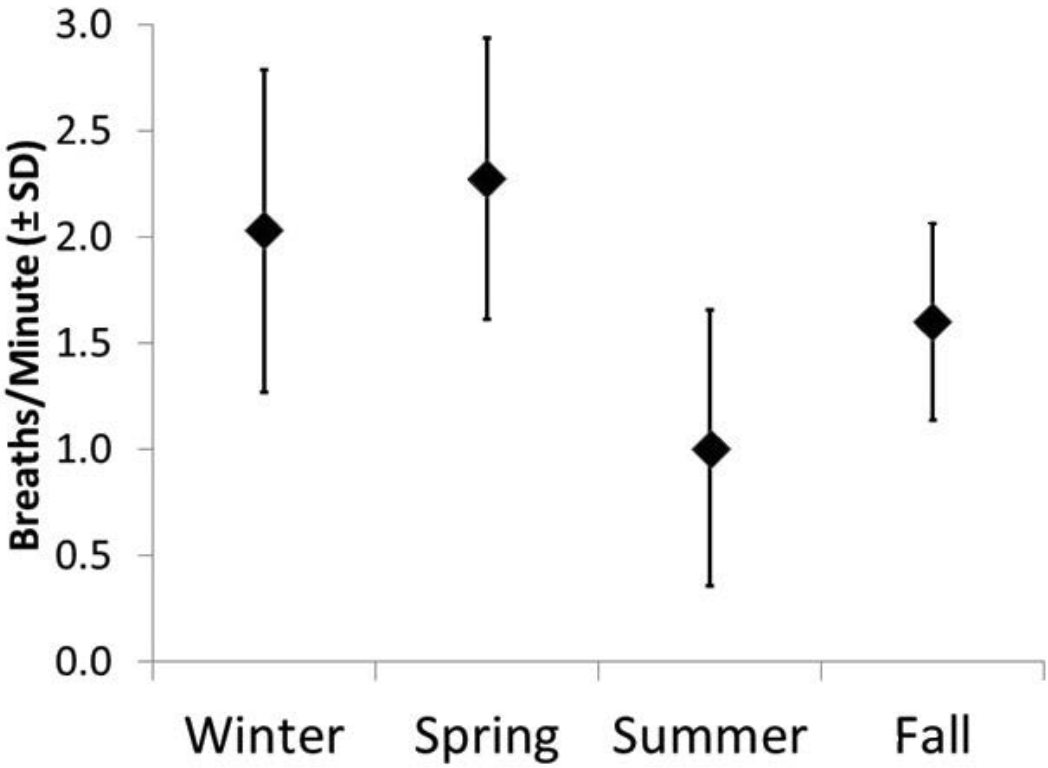

Figure 1. Average respiration rate (± SD) of beluga whales (*Delphinapterus leucas*) as a function of season

Table 1. Average respiration rate (breaths/min) in beluga whales (*Delphinapterus leucas*) ± SD as a function of age and sex

	Males	Females	Sexes Combined
Adults	2.35 (±1.96)	1.30 (±0.97)	1.46 (±1.23)
Calves	1.80 (±1.11)	2.29 (±0.98)	2.05 (±1.07)
Age combined	2.00 (±1.50)	1.55 (±1.06)	1.67 (±1.21)

= 1.54; female $\bar{x}$ = 0.67, SD = 1.01) and least prominent during winter (male $\bar{x}$ = 2.17, SD = 1.89; female $\bar{x}$ = 1.95, SD = 1.21).

- *Season by Age* – A significant season by age-group interaction ($F_{(3, 1,774)} = 31.3$, $p < 0.001$) reflected the fact that decreases in respiration rate in summer were far greater for adults than for calves.
- *Sex by Age* – The sex by age interaction was not statistically significant ($F_{(1, 1,774)} = 1.0$, $p = 0.31$). Nevertheless, it is evident from the averages presented in Table 1 that the overall sex difference reported above derived primarily from the adults.

The following additional analyses were also conducted separately from the above:

Calf/Mother Ratio

The calf/mother respiration-rate ratios are plotted in Figure 2 as a function of calf age. The ratio gradually decreased with age, approaching 1 by the third year of life. The trend line of best fit was curvilinear (y = -0.915 ln[x] + 6.9356; R^2 = 0.33). In a separate GLMM analysis, the natural log transform (y = ln[x]) of the calf/mother ratios were found to be significantly related to calf age ($F_{(1, 409)} = 53.5$, $p < 0.001$).

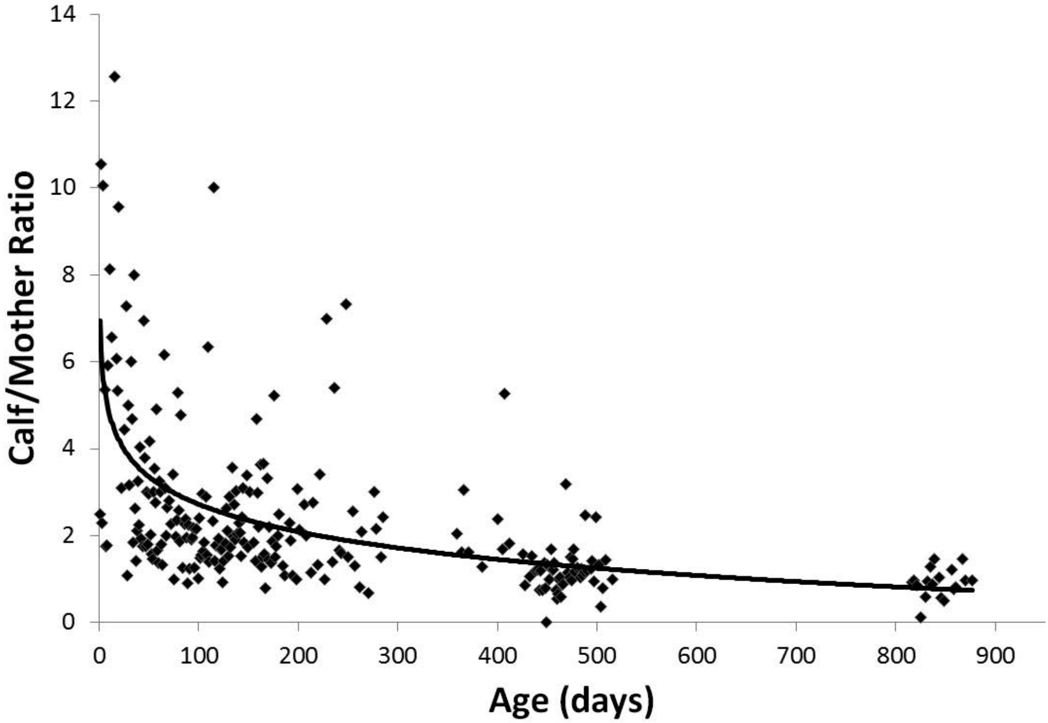

Figure 2. Beluga calf respiration rate, divided by mother respiration rate, as a function of calf age (trendline y = -0.915ln[x] + 6.9356; $R^2 = 0.3252$)

Size

Since sex, age, and size covary, the relationship between body size and respiration rate was examined in one sex at a time and only among adults. In both sexes, respiration rate was negatively correlated with body size. However, this effect reached statistical significance only in females (N = 23, r = -0.549, $p < 0.007$), where the relationship was stronger and the number of subjects was greater than in males (N = 8, r = -0.35, ns).

Discussion

One major finding of the present study is the influence of season on respiration rate in belugas. The observed increase from fall to winter may simply reflect an inverse relationship between respiration rate and ambient temperature—a relationship that presumably derives from the higher metabolic demands of maintaining a constant body temperature under cold conditions (Mortola, 2005; Meagher et al., 2008; Rechsteiner et al., 2013). A more direct investigation of the effects of temperature on metabolic and respiration rates in belugas is therefore warranted. To be ecologically relevant, this should include water temperature ranges beyond those experienced at the present facility. A future investigation should also include assessments of blubber thickness, a factor not available in the present study but known to influence temperature regulation in cetaceans (Worthy & Edwards, 1990; Dunkin et al., 2005; Noren & Wells, 2009).

However, an alternative interpretation of the observed seasonal variation could derive from the fact that beluga whale breeding activity is concentrated in late winter/early spring (Sergeant, 1973; Heide-Jørgensen & Teilmann, 1994; Glabicky et al., 2010). On the assumption that sexual activity is associated with elevated respiration rates, the decrease observed for females during the summer months can be viewed as corresponding to their lack of sexual activity during those months. That a similar decrease was less evident in the males, reflected in the sex-by-season interaction, may derive from the continuing sexual activity which males pursue among themselves during summer months (Glabicky et al., 2010).

Since the respiration rates of the juveniles also rose and fell with the seasons, and also varied from pool to pool and across observation periods, it is particularly difficult to visualize developmental trends in the raw data. By contrast, since mothers and calves were always housed together, considering calf respiration rate as a ratio of mother respiration rate has the advantage of subtracting out the effects of season and particular pool conditions. These ratios showed a particularly elevated respiration rate for the calves immediately postpartum, followed by a gradual decline to the point where the respiration rates came to equal those of their mothers by their third year of age (Figure 2). In this respect, it is notable that this corresponds to the age at which young bottlenose dolphins appear to attain mature diving physiology (Noren & Edwards, 2007), and it is also the approximate age at which both dolphins and belugas discontinue nursing from their mothers (Noren & Edwards, 2007; Pomeroy, 2011).

As a general rule, respiration frequency decreases with body size among adults, both across and within species (Peters, 1983), and that pattern was borne out within each sex in the present study. Given that general trend, and the fact that male belugas tend to be larger than females (Doidge, 1990), the males in the present study might have been expected to have lower respiration rates than the females. In fact, the results trended in the opposite direction. Since respiration rate can be taken as a rough index of metabolic rate (Peters, 1983; Osborne & Milsom, 1993; Rosen & Trites, 2013), the higher respiration rates observed for males suggest that male belugas may have higher metabolic rates than do females. If so, that would correspond to similar findings seen in other species (e.g., Ono & Boness, 1996), including humans (Arciero et al., 1993).

The finding that the newborn/juvenile belugas have higher respiration rates than those of the adults is not surprising in that it matches a widespread pattern among animals generally (Mortola & Noworaj, 1985), and in marine mammals specifically (Miller & Irving, 1975; Lavigne et al., 1986; Thompson et al., 1987; Kastelein et al., 1990; Peddemors, 1990; Mann & Smuts, 1999; Dearolf, 2003). This presumably relates to the fact that the metabolic demands of young animals, even when adjusted for body size, exceed those of older ones (Iliff & Lee, 1952; Miller & Irving, 1975; Thompson et al., 1987; Fleming et al., 2011).

The fact that newborn beluga whales rise to the surface to breathe at a rate three or more times greater than their mothers presents no particular difficulty for the maintenance of mother/calf associations in captivity, where artificial pools are shallow and vertical distances are limited. But in the wild, the different rates at which the members of a pair need to rise to the surface may present a challenge for pair-bond maintenance. Observations on the coordination of maternal dolphins with their calves suggest that they restrict their movements to remain close to their calves (Mann & Smuts, 1999; Noren & Edwards, 2007; Noren, 2008). By contrast, maternal sperm whales often leave their calves at the surface while they carry out deep dives (Whitehead, 1996). It will be interesting to see if maternal belugas in the wild voluntarily restrict themselves to relatively shallow diving patterns in order to afford their calves frequent opportunities to visit the surface while still maintaining sufficiently close contact with their mothers.

In humans, the species in which the factors influencing respiration rate have been most extensively studied, the developmental course of infant respiration rate is related in part to the percent of lung volume exchanged (Carlsen et al., 1994), a factor that increases with age (Hislop et al., 1986; Dezateux & Stocks, 1997). That respiration rates in beluga calves approach those of adults by 3 y of age, a time when calves are still markedly smaller in size than adults, perhaps suggests that critical air-exchange performance variables for the juveniles of this species approximate those of adults by that age. If so, that would appear to approximate the same time course of respiratory development in bottlenose dolphins (Noren et al., 2004; Noren & Edwards, 2007).

In closing, the data presented here add to the growing body of literature documenting the behavior of beluga whales in captivity (e.g., Hill et al., 2013), and it is hoped that these findings improve our understanding of the physiology of this species by illuminating the effects of season, sex, age, and body size on respiration rate.

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