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Synchronous breathing by pilot whales

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When two or more animals behave synchronously, then, unless they are both independently responding to some external stimulus, they are attempting to match to each other's behavior, or at least one is trying to match the other's behavior. Synchrony can thus be a particularly clear example of integrative behavior (Whitehead 2008), and so synchronous behavior can be used to indicate affiliative relationships among individuals and thus to build models of social structure. Synchrony has been described in a range of animal groups, including odontocete cetaceans (Norris and Dohl 1980, Heimlich-Boran 1988, Whitehead 1996, Mann and Smuts 1999, Hastie *et al.* 2003, Connor *et al.* 2006, Perelberg and Schuster 2008, Sakai *et al.* 2009).

Synchrony has been defined in two principal ways: a nonrandom, overly clustered, temporal distribution of behavior among members of a group (Whitehead 1996, Hastie *et al.* 2003), and simultaneous behavior by individual group members (Connor *et al.* 2006). As no two actions are actually absolutely simultaneous, these two definitions are not completely distinct. Rather their usage reflects different research emphases. In the first the degree of temporal synchrony is measured and analyzed (*e.g.*, Hastie *et al.* 2003), whereas in the second the temporal matching is assumed and data collection concentrates on issues such as the identities of the participants and their social and environmental circumstances (*e.g.*, Connor *et al.* 2006). Both types of study give insight into the function of synchronous behavior.

In cetaceans, as well as in other animals, a range of functions have been suggested for synchronous behavior. These include a signal for cooperation or to reduce tension (Connor *et al.* 2006), which may be more manifested at times of stress (*e.g.*, Hastie *et al.* 2003). Rather more prosaically, synchrony may be an artifact of swimming in close proximity, commencing a cyclical behavioral sequence at the same time (Whitehead 1996), or a method of reducing hydrodynamic drag (Weihs 2004). In bottlenose dolphins (*Tursiops* spp.), the cetaceans for which synchrony has been most studied, synchrony is sometimes seen as being involved with the advertisement or reinforcement of social bonds (Connor *et al.* 2006, Perelberg and Schuster 2008, Sakai *et al.* 2009).

Here, we describe synchronous breathing by pilot whales (*Globicephala melas*) off northern Cape Breton Island, Canada, and look for social and environmental factors that may explain the synchronicity of their respirations. These indicate possible functions for the synchronous breathing.

Data were collected off Pleasant Bay, Nova Scotia, Canada (46°50'N, 60°47'W) between 2 July and 28 August 2008, from a 10 m commercial whale-watching "vessel of opportunity" (*Double Hook-up*). At least 1,000 pilot whales use the waters off northern Cape Breton Island (Ottensmeyer and Whitehead 2003). Data were arranged into "encounters," which started when the animals were sighted at <200 m from the vessel (at which range we had a reasonable view of the whales) and ended 10 min after the whales had disappeared from sight, if the boat had to return to the harbor, or the captain wished to approach another group of pilot whales separated by more than 200 m from the original one.

Each encounter was assigned to one of four behavioral states: (1) foraging characterized by no directional movements, long dives, tail-out dives, often with feeding birds associated with the whales and little active surface behavior; (2) resting in which the whales travel very slowly (usually <3 km/h), often "logging," with short and shallow dives; (3) traveling with steady directional movements at greater than 5 km/h; or (4) socializing consisting of active behavior with body contact between individuals, no long dives and little or no directional movement. Synchronous breathing, or the lack of it, was not used as a determinant of behavioral state.

During encounters, pilot whale respiration patterns were filmed with a digital JVC HDD EVERIO, 30 GB Hybrid, with a Konica Minolta lens and 35× optical zoom. Video sequences were started when other routine data collection was completed, and whales were within 200 m of the boat. The video sequence ended after 2 min or if the whales moved further than 200 m from the boat. At any time, the closest cluster (animals traveling in the same direction and less than a few body lengths apart, usually containing 2–12 individuals) to the boat was chosen to video. The video sequence might contain one or more surfacings from each of several members of the cluster.

Only the first sequence in each encounter was analyzed. We defined a paired surfacing as two animals no more than a body width apart traveling side by side (*i.e.*, bodies overlapping in the plane perpendicular to their direction of movement) in the same direction, and breathing no more than 3 s from one another (Fig. 1). The 3 s cutoff was chosen because surfacings last about 3 s, and so this cutoff removed the possibility of the same individual being recorded twice. Additionally, pilot whales either surfaced less than 2 s apart, or much more (Fig. 2). If three or four animals surfaced within 3 s, the pair of spatially closest neighbors was chosen for analysis. If no pair was conspicuously closer, then the surfacing was not analyzed. We noted whether the paired surfacing included a calf or was accompanied by a calf (noticeably small animal light gray in color, so less than about 5 yr old). We timed each respiration, in seconds of elapsed time from the start of the video sequence, when the first white foam appeared from the blowhole at the surface (following Lafortuna *et al.* 2003). The lag (τ) between the respirations of the pair was then calculated by subtraction. This could be 0, 1, 2, or 3 s. If whales were breathing randomly with respect to one



Figure 1. Two synchronously surfacing pilot whales accompanied by a calf, from video sequences.

another, $\tau = 0$ s would be recorded half as often as $\tau = 1, 2,$ or 3 s (as if one whale breathed at time 10 s, a pair would be defined if the other whale breathed at times 7, 8, 9, 10, 11, 12, or 13 s, but only the breath of the second whale at 10 s would give a lag of $\tau = 0$ s while either 9 s or 11 s would give a lag of $\tau = 1$ s, *etc.*). Also, the mean actual lag of paired surfacings of individuals recorded with a lag of $\tau = 0$ s will be 0.333 s (as the mean absolute difference between two randomly chosen numbers, x and y , on the interval $[0,1]$ is $\int \int |x - y|.dy.dx = 0.333$), whereas for recorded lags of 1, 2, or 3 s the mean actual lag approximates the recorded lag. Thus, if the number

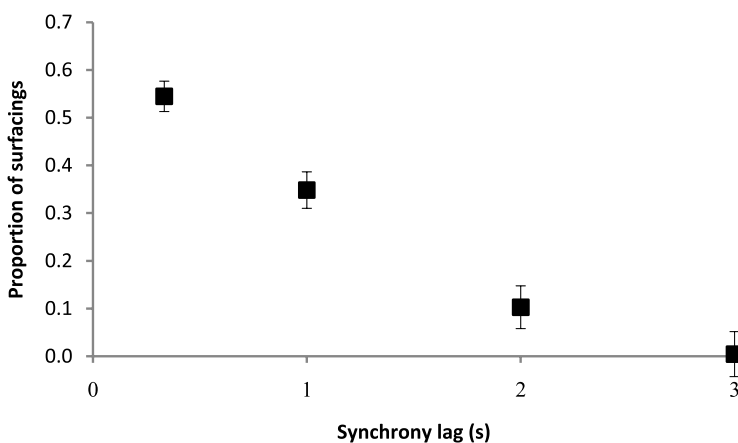


Figure 2. Distribution of time lags in breathing among pairs of pilot whales who surfaced within 3 s. Standard error bars (calculated using binomial approximation) are shown.

of paired surfacings recorded with a lag of τ s was $n(\tau)$, then the probability density of total paired surfacings with a synchrony lag of 0.333 s was estimated as:

$$p(0.333) = \frac{2n(0)}{2n(0) + \sum_{\tau>0} n(\tau)}$$

For a synchrony lag $\tau = 1, 2,$ or 3 s this probability density becomes:

$$p(\tau) = \frac{n(\tau)}{2n(0) + \sum_{\tau>0} n(\tau)}$$

We examined how the synchrony of paired surfacings, indicated by $p(\tau)$, varied with several independent variables: the behavioral state of the animals, the presence of a calf (either as one of the pair, or accompanying a pair of adults), the group size (number of animals present during the encounter), sea surface temperature, the presence of additional whale-watching boats within 200 m of the whales, the time of day and the elapsed time between the start of the encounter and the beginning of the video sequence (a potential indicator of the cumulative stress experienced by the whales from the whale-watching vessel). We also used general linear models to examine the relationship between breath interval, τ , and 38 biologically plausible combinations of these independent variables as well as a control categorical variable indicating the video sequence (which would account for individual, or dyadic, differences in tendencies to synchronize), using Akaike's Information Criterion (AIC) to indicate the fit of each model (Burnham and Anderson 2002). Paired surfacings were the units of analysis.

The data set included 448 paired surfacings collected during 68 encounters on 32 different days. The pairs of whales that surfaced within 3 s generally surfaced 0–1 s apart (Fig. 2) showing that the whales actively synchronized their respiratory behavior (as there is no conceivable external forcing factor). During the video sequences the average, among individuals, of the mean of the intervals between blows made by the same individual pilot whale was 13.2 s ($n = 148$).

The general linear model analysis included 326 paired surfacings, as a few were omitted because of missing values of the independent variables. The best-fitting model (lowest AIC) included just group size (Table 1). However, the addition of behavioral state only increased AIC by 0.67.

The effects of the independent variables on synchrony are shown in Figure 3. At the largest group sizes (30–40 animals) synchrony is increased. Synchrony is reduced when socializing, compared with traveling, resting, and foraging. There is a general trend for synchrony to be more precise in what might be considered more complex or stressful situations: with larger group sizes, with a calf accompanying two adults, with more than one boat present, and longer into the encounter with the whale watch vessel. These independent variables may be related, for instance, if more boats were generally present with longer encounters.

This study was limited by the operational protocols of a whale-watching boat and the video equipment, which had insufficient definition to allow whales to be routinely identified individually. It is clear that pilot whales, like at least some other

Table 1. Fit of general linear models to data on breathing synchrony of pilot whales indicated by AIC. Interval in seconds between breaths of pairs of pilot whales (τ), explained by the continuous independent variables: behavioral state of the animals (BH; categorical), the presence of a calf (TG; categorical), group size (GS), sea surface temperature (SST), the presence of additional whale-watching boats within 200 m of the whales (BOAT), time of day (TIME), and the elapsed time between the start of the encounter and the beginning of the video sequence (TBV).¹ “(X)(Y)” indicates an interaction between variables X and Y. Only models with AIC less than 4.0 greater than that of best fitting model (Burnham and Anderson 2002) are listed.

Model	AIC
$\tau = \text{GS}$	696.14
$\tau = \text{BH} + \text{GS}$	696.81
$\tau = \text{Constant (no independent variables)}$	697.33
$\tau = \text{TBV}$	697.62
$\tau = \text{TIME}$	698.00
$\tau = \text{BOAT} + \text{GS}$	698.02
$\tau = \text{GS} + (\text{TG})(\text{BH})$	698.02
$\tau = \text{TG} + \text{GS} + (\text{BH})(\text{SST}) + (\text{BH})(\text{TBV}) + (\text{GS})(\text{SST}) + (\text{TBV})(\text{GS})$	698.76
$\tau = \text{BOAT}$	698.85
$\tau = \text{SST}$	698.89
$\tau = \text{GS} + (\text{TG})(\text{BH}) + (\text{TG})(\text{SST})$	698.98
$\tau = \text{TBV} + \text{BOAT}$	699.27
$\tau = \text{TG} + \text{GS}$	699.90

¹A categorical variable, the video sequence identifier, was used in seven models but the AICs of these models were well above that of the best-fitting model.

delphinids (Norris and Dohl 1980, Heimlich-Boran 1988, Hastie *et al.* 2003, Connor *et al.* 2006), actively synchronize their respirations. If surfacing within the same 3 s, they preferentially surface within the same second. A number of lines of evidence show pilot whales to have complex and important social systems (Amos *et al.* 1993, Ottensmeyer and Whitehead 2003, De Stephanis *et al.* 2008), and so, given the links between sociality and synchronicity previously suggested for odontocetes (Connor *et al.* 2006), it is perhaps no surprise that synchronization is part of their behavioral repertoire.

Our data suggests that one aspect of this synchrony, the time interval between the respirations of the different individuals, varies with circumstances. In general, the interval between the respirations of two pilot whales decreased in more complex or stressful situations, perhaps signaling cooperation or reducing tension, as suggested for bottlenose dolphins by Hastie *et al.* (2003) in their study of changes of synchrony with boat traffic, and Connor *et al.* (2006), who found synchrony among members of male alliances to be more common in more highly social situations.

In our study area, social units of pilot whales, which have nearly permanent membership, are estimated to contain an average of about 11–12 animals (Ottensmeyer and Whitehead 2003). Synchrony did increase with group size greater than about 30 animals, indicating the presence of several “social units,” and thus a more complex and potentially stressful social environment. Hastie *et al.* (2003) also found synchrony to increase with the group size of bottlenose dolphins in Scotland.

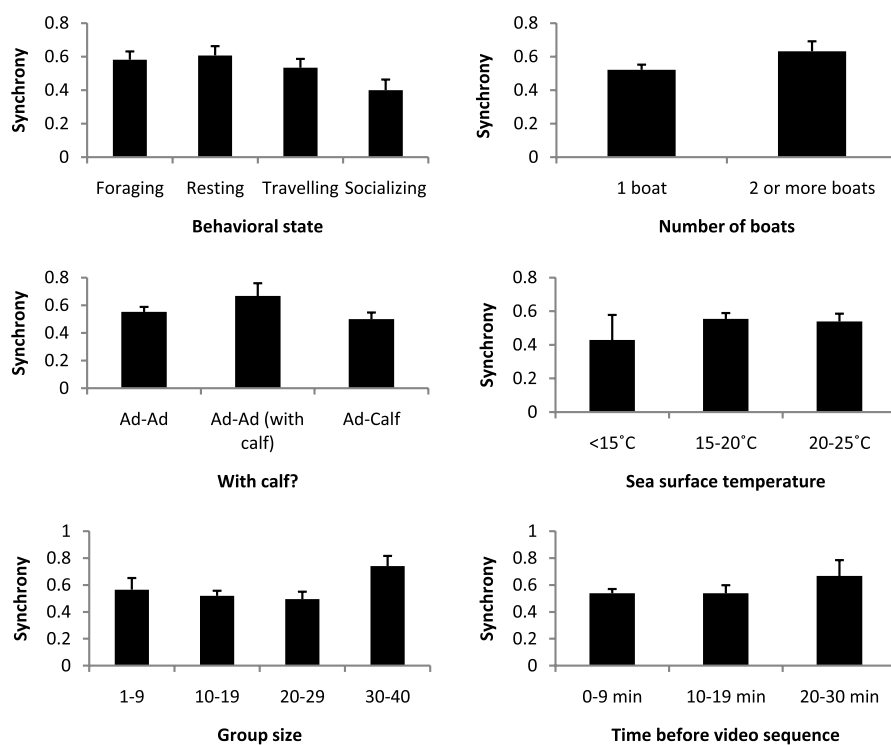


Figure 3. Synchrony, as indicated by proportion of pairs of pilot whales surfacing within 3 s of one another that surfaced within 1 s, by behavioral state, presence of calf, number of boats in attendance, sea surface temperature, group size, and time into encounter at which video sequence started. Standard error bars (calculated using binomial approximation) are shown.

While synchronous breathing could be a specific signal, our data perhaps support the more general function of reinforcing social bonds (Perelberg and Schuster 2008, Sakai *et al.* 2009). Such reinforcement is likely to be more important at times of stress. Synchronous breathing in pilot whales does not seem to be purely an artifact of maintaining proximity (see discussion in Connor *et al.* 2006), as animals maintaining proximity do not need to breathe <1 s apart rather than 1–3 s apart. Highly synchronous breathing may give hydrodynamic advantages but not if the animals are side-by-side, as in most of our data (*e.g.*, Fig. 1; Weihs 2004).

Our study suggests that breathing synchrony may be a useful, and easily measurable, tool for the study of pilot whale sociality. This will especially be the case when high-definition camcorders allow individual identity to be extracted from videos of breathing pilot whales. It also adds to the growing perspective that measures of synchrony may give us considerable insight into the social structures of cetaceans.

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