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BOTTLENOSE DOLPHINS INCREASE BREATHING SYNCHRONY IN RESPONSE TO BOAT TRAFFIC

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ABSTRACT

To minimize potential impacts of boat traffic on the behavior of cetaceans it is important to assess short-term behavioral responses to boats and interpret the long-term consequences of these. Anecdotal descriptions of synchronous behavior in cetaceans are particularly frequent with reports of individuals within schools surfacing to breathe in a coordinated fashion being common. However, quantitative descriptions are rare. This study begins by quantifying synchronous breathing patterns of bottlenose dolphins off northern Scotland. We investigate possible functions of synchrony such as feeding patterns and presence of calves. We then test whether the presence of boat traffic in an area used intensively by dolphins affects their breathing synchrony. Although the majority of dolphin schools observed showed random breathing patterns, 30.5 % of schools showed synchronous breathing. There was no variation in this behavior with respect to identifiable feeding activities. However, synchrony was significantly negatively related to the presence of calves in the school (χ^2 = 7.17, df = 1, P = 0.007) and significantly positively related to the presence of boat traffic in the study area (χ^2 = 13.85, df = 1, P = 0.0002). Such consistent short-term behavioral responses by dolphins may potentially accumulate to produce longer-term consequences both for individuals and the whole population.

Key words: synchrony, *Tursiops truncatus*, bottlenose dolphin, Scotland, SAC, conservation, disturbance, surfacing pattern, calves, behavior.

Most coastal populations of dolphins live in areas also used for a wide variety of human activities. In particular, motorized vessels are frequently used in these area and often come into close contact with dolphins. This has led to concerns over the potential impacts of boat traffic on dolphin behavior (Wilson *et al.* 1997). Threats include physical injury (Laist *et al.* 2001), changes in swimming behavior (Au and Perryman 1982), and changes in vocalizations (for review see Richardson *et al.* 1995). To mitigate and interpret potential impacts posed by boat traffic, it is important to assess short-term responses to boat traffic and in turn identify their long-term ramifications.

To protect a small and isolated population of bottlenose dolphins off northern Scotland, a candidate Special Area of Conservation (cSAC) has been established in part of the populations range, the Moray Firth. This area is also used intensively by a variety of boats for fish farming, oil transportation, spoil dumping, research, and dolphin watching. To minimize the impacts of these activities, there is a clear need to assess and understand changes in behavior in response to boat traffic within the dolphins core habitats.

Behavioral responses to human activities by most terrestrial animals are relatively easy to document (*e.g.*, Burger 1998). However, as dolphins spend the majority of their lives underwater, inferences about behavior must often be based on observations of surfacing events, especially where underwater visibility is poor. Previous research on a variety of cetacean species has documented behavioral reactions at the surface to boats, including decreases in breathing rate (Janik and Thompson 1996) and interanimal distance (DeNardo 1998, Nowacek *et al.* 2001), increases in swimming speed (Kruse 1991, Nowacek *et al.* 2001) and changes in swimming direction (Au and Perryman 1982, Nowacek *et al.* 2001).

Throughout the literature on cetacean behavior there are descriptions of individuals within schools breaking the water surface to breath in a synchronized fashion (*e.g.*, Würsig 1978, Norris and Dohl 1980, Jacobsen 1986, Heimlich-Boran 1988, Ballance 1990, Shane 1990, Connor *et al.* 1992, Whitehead 1996, Similä 1997, Acevedo-Guiterrez 1999). Synchrony has been linked to a variety of contexts in cetacean behavior including feeding (Similä 1997), socializing (Brager 1993, Hanson and Defran 1993, Möller and Harcourt 1998), and parental care (Whitehead 1996, Mann 1999). Synchrony, therefore, potentially represents an important facet of the behavior of cetaceans at the water surface. However, behavioral synchrony has only been rarely quantified (Whitehead 1996), constraining efforts either to understand its underlying function or the extent to which it may be influenced by the presence of boat traffic.

In many studies describing synchrony, it is not possible to determine whether breathing patterns described really are synchronous; considered here as significant deviation from that expected if dolphins surfaced independently to each other. However, as the act of surfacing to breathe is a discrete, unambiguous event that does not require detailed interpretation by the observer, defining a breathing pattern as synchronous or otherwise is potentially an objective and testable task. This study, therefore, begins by formulating a method to quantify synchronous breathing patterns by individuals within schools of dolphins. We used the resulting data to investigate possible functions of breathing synchrony; variations in the degree of synchrony in specific contexts, such as feeding patterns and presence of calves. We then test whether the presence of boat traffic in a core region of the Moray Firth cSAC affects dolphins breathing synchrony.

Methods

Study Area

These studies were carried out within a 1.2 km^2 area spanning the entrance to the Cromarty Firth, NE Scotland (57°41′ N, 4°00′W). This is a relatively small, coastal channel that is used intensively by most of the 130 individuals in this population of bottlenose dolphins (Wilson *et al.* 1997). The area is used consistently also by a variety of boats including research vessels, commercial and recreational dolphin watching boats, cruise liners, and commercial tugboats.

Field Procedure

Observations of schools of dolphins were made from a 90-m high headland overlooking the study area. Individual schools were videoed using a Canon Ex2-Hi 8 video camera with an 8–120-mm zoom lens and a 2× converter (Canon (UK) Ltd., North Circular Road, London, UK). Schools of dolphins were defined as "aggregations of individuals within 100 m of each other." Schools were selected at random and were video recorded for 10 min. During this period the school was considered a single sample unit. Recording was abandoned if the school dived for a period of >2 min, if the school left the study area or if dolphins left, or joined the school.

Quantifying Synchrony

The video footage of each sample was later reviewed to record the time (to the nearest second) of every dolphin surfacing. A surfacing was defined as the point at which any part of the dolphins body first appears above the surface of the water. To quantify the degree of synchrony in the pattern of surfacings, we counted the number of surfacings in sequential 3-sec intervals (*e.g.*, Fig. 1). This interval of 3 sec was chosen to minimize the likelihood of individual dolphin surfacing twice within one interval and was based on previous literature on bottlenose dolphin dive behavior, which showed that the dive durations of ≤3 sec are rare (*e.g.*, Fortuna 1995).

To test whether or not dolphins were surfacing randomly in relation to the other dolphins in the school, the frequency distribution of the number of surfacings in each 3-sec interval was compared to a binomial distribution. The relative expected frequencies (probabilities of the various outcomes) were calculated using binomial coefficients (Sokal and Rohlf 1981), together with the probability of an individual dolphin surfacing within a 3-sec interval. This probability was calculated from the total number of surfacings observed divided by the product of the estimated school size and the number of 3-sec intervals.[1] It was assumed that all individuals surfaced at the same rate.

The number of 3-sec intervals within a sample was then multiplied by the relative expected frequencies to calculate the absolute frequencies for the expected distribution. The two distributions were compared using a chi-squared goodness

[1] Personal communication from D. Elston, BIOSS, The Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK, 15 August 2000.

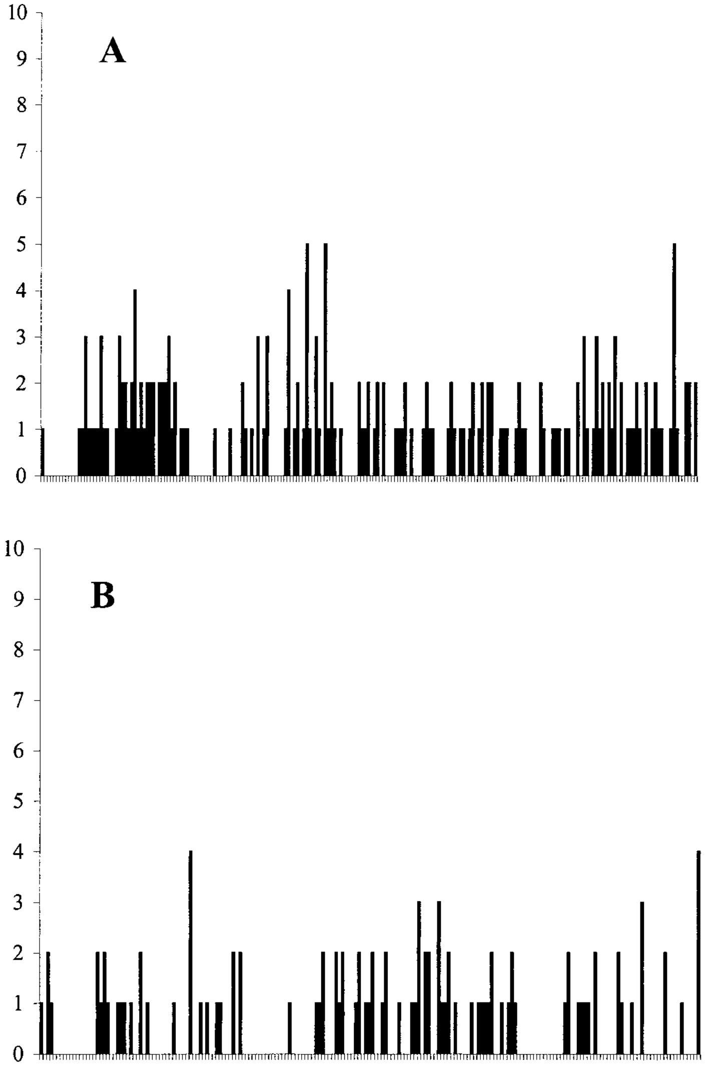

Figure 1. An example of number of dolphins surfacing within consecutive 3-sec intervals over 10-min periods. Graph (A) shows synchronous breathing pattern and graph (B), random pattern. Note that estimated school size in both cases was ten dolphins.

of fit test. If any of the expected values fell below 1, relevant categories were clumped together. When comparing the distribution to a binomial distribution, degrees of freedom were calculated as $a - 2$ (where a is the number of classes after clumping) (Zar 1984). Relevant samples were subsequently defined as significantly different from the binomial distribution at a probability value of 0.05.

To test which "direction" each distribution was skewed, all the samples were subsequently tested to establish whether the observed distribution showed a clumped or uniform distribution by calculating the coefficient of dispersion (Zar 1984). This is a test score that is less than one if the data are evenly distributed, equal to 1 if they are randomly distributed, and greater than 1 when the distribution is clumped. Samples were termed "synchronous" only if their distribution was significantly different to the binomial distribution and if their coefficient of dispersion was greater than 1.

Factors Influencing Synchrony

Logistic regression models (*e.g.*, Cox 1970) were used to explore how the probability of breathing synchrony varied with changes in explanatory variables. Each sample was scored as 0 or 1 depending on whether the breathing pattern was synchronous. These values for each sample were used to represent the level of synchrony and were incorporated as the outcome variable in logistic regression analyses.

The predictor variables used in the analysis were the presence of calves in the school and the incidence of feeding behavior (each sample was scored as 0 or 1, depending upon whether fish were observed at the surface in close proximity to the school). Furthermore, as individual samples had variable durations and dolphins associated with them, there was the potential that these factors alone could inherently affect the probability of a surfacing pattern being synchronous (Speakman *et al.* 1992). To account for this, the sample duration and the school size for each sample were initially included as explanatory variables. To test whether boat traffic was influential in the probability of a surfacing pattern being synchronous, the presence of boat traffic within the study area was included in the analyses. The majority of boats were $<$10 m in length, and it was rare for more than two to be present at any one time. Other vessels that were occasionally in the study area included large commercial tugboats, oil tankers, and cruise liners. Such large vessels rarely spent $>$10 min within the study area, generally moving through on a straight course. However, smaller vessels included commercial and recreational dolphin-watching vessels, and dolphin research vessels often spent over 30 min in the area and would frequently maneuver close to schools of dolphins.

The results presented include a first round of modeling where all variables were considered singly in a logistic regression model. All single variables and their interactions were then considered simultaneously in a final model using the Binomial Logistic Regression procedure in the SYSTAT version 7.0 statistical package (SPSS Inc., Chicago, IL.) with each variable being added to the model on a stepwise basis. To initially account for those variables that were inherently related to the probability of a pattern being synchronous, the variables in the simultaneous model were entered in two blocks. "Sample duration" and "School size" were entered initially; this was followed by entry of the remaining variables and their interactions (Gordon *et al.* 1998). All categorical variables in the analysis were coded as "dummy" variables (Zar 1984).

RESULTS

A total of 128 samples were collected between May and September 1997, 1998, and 1999. Samples were collected at all states of the tide and at all times during daylight hours. The median duration of samples was 3 min (IQ range = 2–7 min).

Table 1. Goodness-of-fit tests for each of the variables fitted individually in logistic model for predicting synchronous surfacing patterns.

Model	L.L. ratio	Change in L.L. ratio (χ^2)	df	*P*
Null	157.385			
Sample Duration	153.398	3.987	1	0.046
School size	144.163	13.221	1	0.0003
Calves	150.258	7.126	1	0.008
Fish sighted	156.994	0.391	1	0.532
Boat traffic	146.727	10.658	1	0.001

Synchronous Breathing Patterns

Forty (31.3%) of the samples had an observed frequency distribution that was significantly different to the binomial distribution. Coefficients of dispersion ranged from 0.69 to 2.92 and the median value was 1.21. Ninety-eight (81.7%) of the samples had coefficients of dispersion greater than one. Of the 40 samples with frequency distributions significantly different to a binomial distribution, only one had a coefficient of dispersion less than one. Consequently, 39 (30.5%) samples showed significantly synchronous breathing patterns.

Factors Influencing Synchrony

Results from the first round of logistic modeling suggested that four of the variables, sample duration, school size, presence of calves, and presence of boat traffic were significantly related to the probability of a breathing pattern being synchronous (Table 1). When all the variables were fitted simultaneously, using a forward stepwise procedure, school size, presence of calves, and presence of boat traffic remained significantly related to the probability of a breathing pattern being synchronous (Table 2). This best fit model predicts that as school size increases, the probability of a breathing pattern being synchronous also increases. There was a significantly lower probability of synchrony in schools with calves, and there was a significantly higher probability of synchrony when boat traffic was present in the study area.

Discussion

These results provide the first quantified data on synchronous breathing patterns within schools of coastal dolphins and provide a field and analytical protocol that could potentially be used in a variety of study areas. Although 69.5% of surfacing patterns were not significantly different to those expected by random chance, this study has shown that schools of bottlenose dolphins within the Moray Firth do frequently show synchronous breathing patterns. This behavior was significantly related to the presence of calves in the school and the presence of boat traffic in the study area. In contrast, there was no variation in this behavior in relation to overt surface-feeding events, suggesting that this synchrony may not be related to feeding. However, observations were made using the video camera from land and it was possible to identify those events only if the fish were

Table 2. Summary of stepwise logistic regression model for predicting synchronous surfacing patterns, including single variables and interactions between variables.

Model terms	L.L. ratio	Change in L.L. ratio	df	*P*	*B*	Exp (B)
Constant					−4.549	0.011
School size	144.163	13.22	1	0.0003	0.38	1.463
Calves	131.87	7.17	1	0.007	−3.357	28.7
Boat traffic	124.7	13.85	1	0.002	1.437	0.236
Rejected terms		Score	df	*P*		
Sample duration		3.403	1	0.065		
Fish sighted		0.843	1	0.359		
Boat traffic × Fish sighted		1.726	1	0.189		
Calves × Fish sighted		0.833	1	0.361		
Boat traffic × Calves		0.447	1	0.504		

fairly large and chased or manipulated at the surface. Therefore, synchrony may still reflect different feeding activities where prey capture occurs away from the surface (*e.g.*, Similä 1997). There was also a significant positive relationship with school size and synchrony. However, it is unclear whether this represents a genuine behavioral relationship or is merely an artifact of the inherent positive relationship between sample size and probability of clustering (Speakman *et al.* 1992).

Given the numerous descriptions of the close-surfacing associations between mothers and calves (Würsig 1978, Ballance 1990, Mann and Smutts 1999), it was interesting that there was a significant negative relationship between the presence of calves in the school and the probability of synchrony. This may be because our assumption that all dolphins surfaced to breathe at the same rate is invalid. Calves appeared to surface to breathe more frequently than adults in the schools and, as such, often surfaced anachronously with respect to the other members of the school. It has also been shown that while there is clear synchronization of the surfacings between mothers and calves during the first month of the calf's life, this quickly decays during the second month of life (Mann and Smutts 1999).

Although the underlying function of this behavior remains unclear, this study has shown that breathing synchrony is clearly influenced by the presence of boats in the study area. The probability of a breathing pattern being synchronous was significantly higher when boats were present. This result is supported by previous studies that have shown that dolphins may exhibit short-term behavioral responses to boat traffic. These include changes in breathing rate (Janik and Thompson 1996) and interanimal distance (DeNardo 1998, Bejder *et al.* 1999, Nowacek *et al.* 2001), increases in swimming speed (Kruse 1991, Nowacek *et al.* 2001) and changes in swimming direction (Au and Perryman 1982, Bejder *et al.* 1999, Nowacek *et al.* 2001). In many of these studies behavioral changes were considered short term escape responses to boats.

Although it is easy to interpret behavior such as increases in speed and changes in direction as escape behavior, the function of an increase in breathing synchrony is far less clear. However, group living by many species commonly acts to reduce the risk of predation (Pulliam and Caraco 1984, Inman and Krebs 1987) and synchronous behavior is commonly observed in these species.

Coordinated "wheeling" by flocks of birds for example, is thought to function as an antipredator device. Similarly, air-breathing fish such as walking catfish (*Clarias batrachus* and *C. liocephalus*) have been observed breathing at the water surface synchronously (Kramer and Graham 1976, Loftus 1979, Chapman 1994). These species are subject to heavy predation by birds, and it has been suggested that respiring in this synchronous fashion may help to reduce an individual's chance of being caught by a bird. Furthermore, synchrony in the emergence of pipistrelle bats (*Pipistrellus pipistrellus*) from their roosts was thought to be a functional response to predation (Speakman *et al.* 1992) and the synchronous foraging behavior of groups of Yakushima macaques (*Macaca fuscata yakai*) was also thought to reduce predation risk and maintain the spatial cohesion of the group (Agetsuma 1995).

It is therefore possible that dolphins in this study area consider boats as a threat and synchrony does form part of a antipredatory type of response in dolphins when in the presence of boats. Some authors have recorded decreases in interindividual distance at the surface in response to approaches by boats (*e.g.*, Au and Perryman 1982, Blane and Jaakson 1994, Bejder *et al.* 1999). However, there is an intrinsic link between the spacing of individuals at the surface and breathing synchrony; as synchrony increases, the interindividual distance will decrease. It is possible, therefore, that the observed decreases in spacing observed in these studies (Au and Perryman 1982, Blane and Jaakson 1994, Bejder *et al.* 1999) are in fact due to increases in breathing synchrony in response to boats.

Most of the dolphins in this population are sighted regularly within this small study area over periods of several years (Wilson *et al.* 1997). Consequently, they are likely to come into regular close contact with boats. This implies that the behavioral response may not play a role in an escape response, but that the presence of boats may actively influence the behavior of the dolphins. For example, it is possible that engine noise might mask certain dolphin calls making it less efficient for dolphins to communicate or forage acoustically while boats are present (*e.g.*, Van Parijs and Corkeron 2001). Synchrony may, therefore, play a role in the social cohesion of the school during periods when it is less efficient to communicate or forage acoustically. Alternatively, it is possible that changes in dolphin behavior reflect changes in the behavior of fish around boats (Gerlotto and Fréon 1992, Engas *et al.* 1995, Janik and Thompson 1996). For example, Engas *et al.* (1995) showed that cod react to the sound of boat engine noise by schooling together and swimming toward the seabed.

Although the function of synchrony in response to boat traffic in this study remains uncertain, it is clear that dolphins respond to the presence of boats in this core region of the Moray Firth cSAC. This has important consequences for the conservation and management of this population of dolphins. The study area is used intensively by a high proportion of this population of dolphins throughout the year (Wilson *et al.* 1997, Hastie 2000). Consistent short-term behavioral responses by dolphins could therefore accumulate to produce longer-term consequences for these animals, if they are frequently surfacing to breathe at an energetically inefficient rate, or are consistently precluded from important behaviors such as foraging. As the area is also an important waterway for human activities, future monitoring should assess the use of the area by boat traffic and dolphins and determine how best to minimize potentially detrimental interactions between them.

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