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Change in southern right whale breathing behavior in response to gull attacks

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Abstract Animals may develop behavioral responses to avoid discomforting situations. In particular, pain can result in learned avoidance behaviors. We report such a case in southern right whales (*Eubalaena australis*) that have been the target of attacks by kelp gulls (*Larus dominicanus*) that feed on their skin and blubber in the surrounded waters of Península Valdés, Chubut (Argentina) since the 1980s. The increase in the attacks over the years triggered on whales the development of alternative postures to keep their backs protected from the gulls. Recently, a particular avoidance behavior has been observed, the "oblique breathing," in which whales breathe with only the head out of the water. The main goal of this work is to describe the emergence of oblique breathing in two areas of Golfo Nuevo (P. Valdés) which have high number of whales and gull attacks, during the whale reproductive seasons in 2010, 2012 and 2013. Results suggest that all age and sex classes of whales can breathe obliquely. Emergence of the oblique breathing seems to have proceeded in three stages: (1) the origin, with rare observations, (2) the spread, when the behavior was registered only during gull attacks and (3) the establishment, when whales performed it in a preventive manner, even when attacks were not occurring. Oblique breathing is likely to pose extra energy costs, which could be detrimental to whales, especially for recently born calves. However, given the increasing prevalence of this behavior, it seems to be a useful strategy to prevent harassment by gulls.

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Introduction

All animals possess innate motor patterns that in many species interact with experience and learning to form behaviors (Grandin and Deesing 1998). Generally, young animals begin their lives with few well-developed behavioral patterns. Most behavioral traits develop under the influence of postnatal environmental stimuli and are strongly affected by learning (Domjam 2009; Cabrera and Dos Santos 2012). Pain is one of the primary sensations that comes directly from the activity of the sensory receptor cells and, without involving high levels of brain processing as fear does, produces a significant response. Pain produces both protective motor and vegetative reactions (Broom and Johnson 1993). In addition, pain can result in behaviors learned through what is known as negative reinforcement, i.e., a type of conditioning that promotes behavior to avoid or escape aversive stimuli (Cabrera and Dos Santos 2012).

Differences among individuals in their propensities for learning can have important fitness consequences (Caro and Hauser 1992). Most studies of learning in marine mammals have been focused on foraging and feeding behaviors. Feeding conditions are often more easily quantified than many other behaviors and they are also essential to the survival and fitness of individuals (Mithen 1999). For example, killer whales (*Orcinus orca*) use, for some feeding behaviors, social transfer through apprenticeship, one of the mechanisms that enable a high degree of adaptability (Guinet and Bouvier 1995). Another example is the lobtail feeding method developed by humpback whales (*Megaptera navaengliae*), which was most likely acquired through social transmission (Allen et al. 2013). It has been shown that marine mammals learn behavioral strategies to avoid and deal with predators (Pitman et al. 2001; Gowans et al. 2007). However, marine mammals, as any animal species, can experience a discomfort situation that is not necessarily a predation risk, but generates a change in the behavior. If this change allows avoiding or dealing with the discomfort situation, it could be learned by other conspecifics through social transmission.

In Península Valdés, Patagonia Argentina, kelp gulls (*Larus dominicanus*) rip skin and blubber from the back of the southern right whales (*Eubalaena australis*) to feed (Thomas 1988; Rowntree et al. 1998; Fazio et al. 2012), causing them painful wounds (Fazio et al. 2012; Bastida 2013). The relation between these two species is considered as a facultative temporary parasitism since gulls are generalist and opportunistic feeders that attack whales only in the whale reproductive season in Península Valdés, when they are in their home range. The first records of gull attacks on whales were occasional (Cummings et al. 1972). However, in the 1990s, the gull and whale population sizes increased and so did the interaction between these two species. Thereafter, these "attacks" have become more frequent and intense, and they have spread geographically (Rowntree et al. 1998; Fazio et al. 2012). Now a days, gull attacks are so widespread in waters surrounding Península Valdés that it seems that there is no place without this interaction. Although it is possible to see gull attacks on both adult whales and calves, the latter are the main targets (Fazio 2013).

Most whales react to gull attacks with strong exhalations and a flinch, submerging the back and raising the head and tail simultaneously in rapid motion (Thomas 1988). Many times this flinch extends in time as a secondary response to avoid the attacks. This behavior, called "crocodiling" (Thomas 1988) or "galleon position" (Sironi et al. 2008), leaves the whale resting on the surface with the head and tail high, but the central part of the back submerged. Thomas (1988) also described a resting behavior that he called "head visible," which consists of moving slowly or not at all leaving only the dorsal part of the head on the surface.

In recent years, whales have showed a noticeable new behavior in response to the continuous harassment by gulls. We call this behavior "oblique breathing." The aim of this paper is to describe and quantify this new behavior in two coastal areas of Península Valdés.

Materials and methods

Observations were made in two areas of Golfo Nuevo called "Puerto Pirámides" and "El Doradillo" (located about 70 km apart), during the southern right whale breeding seasons between 2009 and 2013 as part of the project studying the gull attacks that started in 2005. In Puerto Pirámides, observations were made from whale-watching vessels that operate from Puerto Pirámides town (42°34′S, 64°16′W; Fig. 1), along a 25-km stretch along the coast, from June to December, taking advantage of the attack data collection already ongoing. A small kelp gull reproductive colony (with around 500 breeding pairs) is located nearby, in Punta Pirámide (Fig. 1). During each trip, boats often stop several times to observe a whale or groups of whales. Each stopover was considered a "sighting," defined as the observation that took place when the boat stopped or stayed at least 1 min at a distance of around 50 m from one or more whales. The numbers of sightings in a single trip ranged from 1 to 11, with varying durations. Between 60 and 70 % of these sightings involved cow–calf pairs (Fazio 2013). In El Doradillo, observations were made along a 5-km stretch along the coast, from a viewpoint located on the edge of a cliff (Punta Flecha, 42°38.6′S, 64°58.2′W; Fig. 1) between July and October. This area not only has a high concentration of whales (as in Puerto Pirámides), but also acts as an air corridor for the gulls that fly from their nesting sites [the largest is at the Islote Notable and has more than 4,000 breeding pairs (Lisnizer et al. 2011)] to the dumps to feed. The observations, also called sightings for comparison with those in Puerto Pirámides, were collected by following a whale or group of whales with a telescope 20–60 × (SWIFT MARK II) with an operating range up to 2,000 m from the coast. Sighting duration ranged between 14 and 16 min. In this area, almost 90 % of the sightings involved cow–calf pairs, reflecting the prevalence of this group type in the area (Fazio 2013). In both cases, consecutive sightings were always done with different whales or group of whales in order to have independent gull or attack scenarios.

Gull attacks on whales were recorded in all study years. Each attack was defined as the event where a gull pecked any exposed body section of a whale, settling on it or not. While the largest number of attacks was made on the dorsal area of the whale between the posterior section of the blowhole and the beginning of the caudal peduncle, some were recorded in other parts of the body. An example of this are pecks made on the callosities in the head, where a large number of cyamids (i.e., arthropods that feed on the dead skin of whales) are housed and which also constitute a source of food for gulls (Cummings et al. 1972). Attack rate (No. of attacks h^{-1}) was defined as the number of attacks in a single sighting divided by the duration of the sighting in hours.

Two whale postures were monitored on target whales. During "oblique breathing," a whale emerges only its head up to the blowhole to breathe, while the rest of the

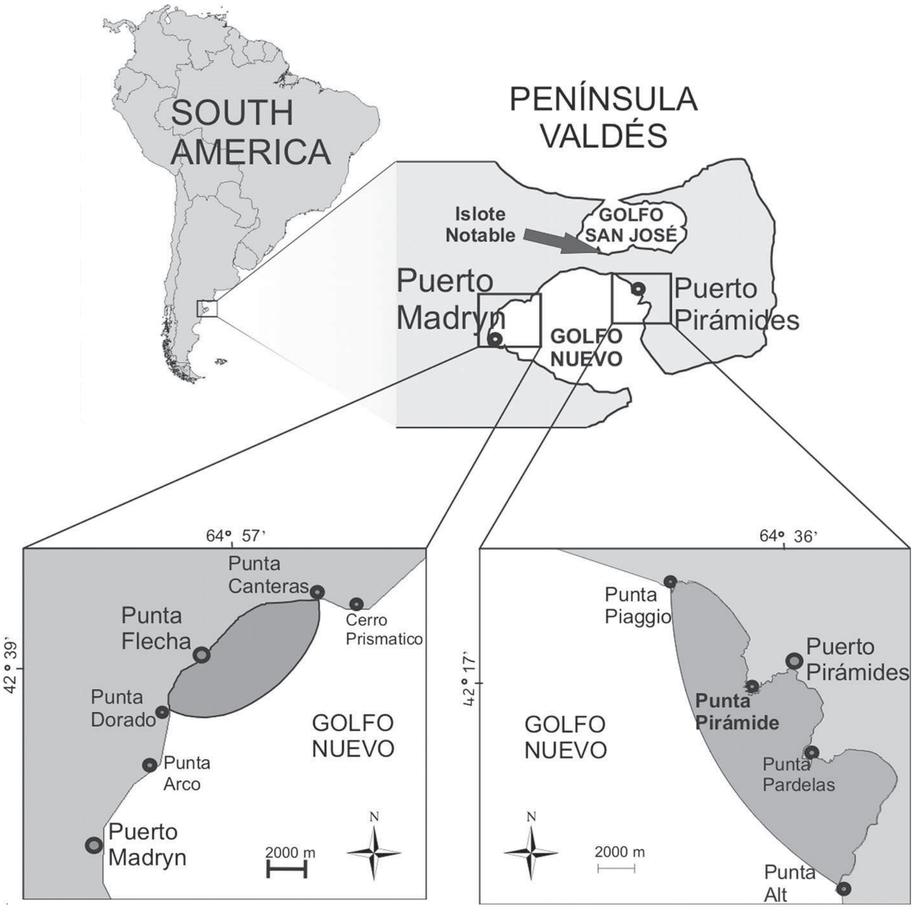

Fig. 1 Main study areas (*dark gray*) in Golfo Nuevo, Península Valdés, Argentina. *Bottom right*: from boats operated from Puerto Pirámides; *bottom left*: from coast in Punta Flecha (ANP El Doradillo)

body remains under water. After a breath, the whale submerges completely. Typically, the head emerges vertically or at an angle of about 45° to the sea surface. Most of these breaths are short, strong and repetitive, and some of them are accompanied by a low-frequency sound. A whale that is performing oblique breathing is not resting and, most times, is moving quickly. An example of a sequence of oblique breathing of a mother and calf under attack is given in Online Resource 1. If one of the target whales of the sighting did five or more consecutive oblique breaths, the sighting was considered with (presence) oblique breathing. This definition excludes, for example, cases in which whales breathe obliquely once or twice after a sequence of breaches that are not related to gull attacks. Oblique breaths are mostly consecutive but sometimes interspersed with normal breaths. In addition, in 2013, the actual number of oblique breaths was recorded for each oblique breathing event. The second posture was the galleon position defined earlier (Sironi et al. 2008). In this case, the presence or absence of sustained galleon position (for at least 1 min) of at least one of the target whales in a sighting was recorded. Less than one minute duration of galleon position was not considered as such in case it was due to another reason other than avoiding attacks. Age class and sex of these whales were also identified whenever possible. The presence of oblique breathing made by mother or calf, number of attacks and the body part attacked (i.e., the callosities or the back) were also recorded for sightings performed in 2012 and 2013 (Table 1). In addition, in 2013, the number of normal and oblique breaths in both adults and calves was registered in several whales of the sightings (Table 1).

In order to compare oblique breathing frequencies in the two study areas (El Doradillo and Puerto Pirámides), only sightings that involved mother–calf pairs and, in the case of Puerto Pirámides, only 14- to 16-min-long sightings taking place within 2,000 m of the shore were taken into account for some analyses.

All statistical analyses were performed using SPSS 15.0.1 for Windows. Variance homogeneity of data sets was assessed using Levene test in order to determine the use of parametric or nonparametric analyses.

Results

The percentage of sightings with oblique breathing increased along the years (Table 2). In El Doradillo, the differences were significant between years (Likelihood ratio

Table 1 Whale behaviors registered in each sighting in the two areas of the different studied years

Whale behavior	Year			
	2006–2008	2009–2010	2012	2013
Presence of galleon position	Pir	Dor	Pir and Dor	Pir and Dor
Presence of oblique breathing	ND	Dor	Pir and Dor	Pir and Dor
Presence of oblique breathing in mother or calf separately	ND	ND	Pir and Dor	Pir and Dor
No. of oblique and normal breathing in mother or calf separately	ND	ND	ND	Dor

Dor Doradillo; *Pir* Puerto Pirámides; *ND* no data

Table 2 Percent of the sightings that involved mother–calf pairs where oblique breathing, attacks and attack rates were recorded, comparing study years and areas

Year	Area	% sightings with oblique breathing	% sightings with attacks	*G* test values	*P* values	Attack rate (X ± SD)	*N*
2010	Dor	2.8	68.9	−63.9	<0.001	14.05 ± 16.51	322
2012	Dor	14.5	57.9	−136.6	<0.001	15.66 ± 40.14	304
2012	Pir	15.6	53.1	−16.16	<0.001	9.03 ± 14.49	32
2013	Dor	69.4	71.8	387.7	<0.001	18.33 ± 24.11	340
2013	Pir	22.4	43.5	−45.95	<0.001	6.64 ± 10.47	85

G tests and *P* values correspond to the dependence between the sightings with oblique breathing according to the presence or absence of attacks (in Puerto Pirámides, *G* test values incorporated Yates' correction)

Dor Doradillo; *Pir* Puerto Pirámides

test, $G2 = 426.6$, $P < 0.001$), whereas in Puerto Pirámides, they were not (Likelihood ratio test, $G1 = 0.3$, $P = 0.6$). The percentages of sightings with oblique breathing in both areas during 2012 were similar (Likelihood ratio test, $G1 = 0.03$, $P = 0.86$), while those during 2013 were higher in El Doradillo (Likelihood ratio test, $G1 = 63$, $P < 0.001$). Besides, the sightings with oblique breathing depended on the presence of attacks in both areas in all the studied years (Likelihood ratio test, *G* values in Table 2, all $P < 0.001$). On the other hand, the attack rates were higher in El Doradillo within each year (Table 2), but these differences were significant only in 2013 (Mann–Whitney *U* test, $U = 9373.5$, $N1 = 340$, $N2 = 85$, $P < 0.001$). Gathering both areas and years (2012 and 2013) together, the sightings with oblique breathing had a mean attack rate of $X \pm SD = 21.25 \pm 37.44$ attacks h^{-1}, $n = 304$, while the ones without oblique breathing had a mean attack rate of $X \pm SD = 11.79 \pm 24.37$ attacks h^{-1}, $n = 457$, and these values were significantly different (Mann–Whitney *U* test, $U = 50266.5$, $N1 = 457$, $N2 = 304$, $P < 0.001$).

Considering only the sightings with attacks (to calves or mothers), a positive correlation between the frequency of sightings with oblique breathing and the attack rate was observed (Spearman rank correlation, $rs = 0.975$, $N = 5$, $P < 0.001$) in El Doradillo during the 2012 whale season

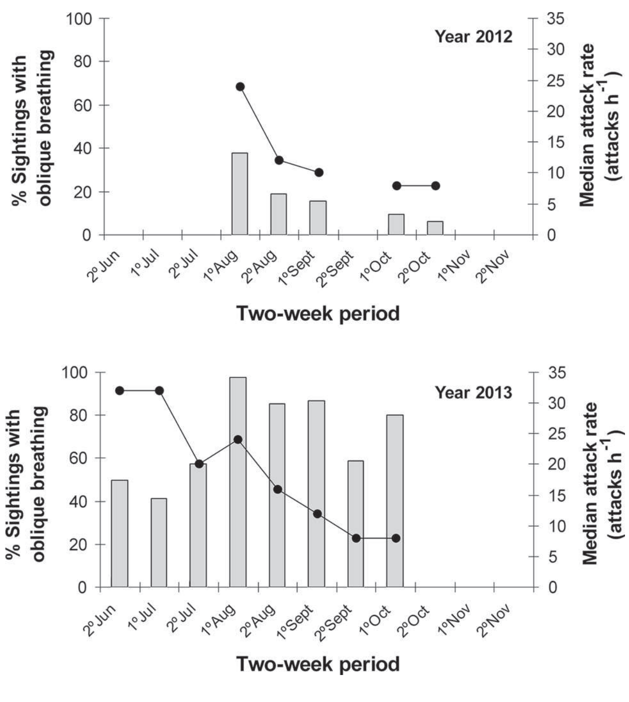

Fig. 2 Percentage of sightings with oblique breathing (*left ordinate axis*, *bars*) and median values of attack rates (*right ordinate axis*, *solid line*) for the sightings with attacks during the whale season in El Doradillo in 2012 and 2013. Two-week periods without value had no data

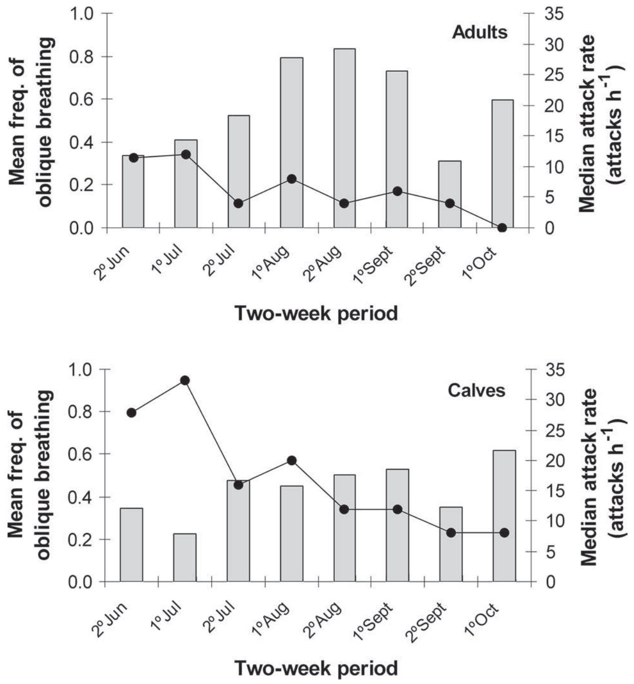

Fig. 3 Mean average frequency of oblique breaths (No. of oblique breaths over the total no. of breaths at each sighting) in *left ordinate axis* (*bars*) and median values of attack rates of the sightings with attack (*right ordinate axis*, *solid line*) throughout the whale breeding season in El Doradillo in 2013

(Fig. 2). However, during 2013 season, it was not significant (Spearman rank correlation, $rs = -0.434$, $N = 8$, $P = 0.283$).

Considering the number of oblique breaths (recorded only in 2013), and separating in adults and calves, the mean frequency of oblique breaths of adults was higher in August and the first half of September, even when a lower intensity of attacks was recorded (Fig. 3). On the other hand, the mean frequency of oblique breaths of calves slightly increased (except in the second half of September), but the intensity of attacks decreased along the season and had higher absolute values than the ones in adults (Fig. 3). During the whole period, we only observed the galleon position in adult female whales, both mothers with calves and pregnant females. However, the oblique breathing was registered in all whale categories, including adult males, adult females, solitary individuals and calves (Table 3).

Discussion

The oblique breathing behavior possibly emerged between 2008 and 2009. Since 2005, gull attacks have been recorded, but it was not until 2008 that oblique breathing was first observed. Since 2009, this behavior was specifically monitored, and not only adults (males and females) but also calves showed it. This behavior could have derived from the behavior described by Thomas (1988) as "head visible," which unlike oblique breathing is a posture that whales seem to perform when they rest or travel slowly. The oblique breathing behavior could have emerged to avoid the attacks from gulls, which developed a feeding behavior on skin and blubber of whales, causing them painful wounds (Fazio et al. 2012).

The incidence of oblique breathing increased significantly since it was first recorded in 2009. In El Doradillo, the frequency of occurrence of this behavior has quintupled between 2010 and 2012 and again increased fivefold between 2012 and 2013. Precisely in this area, the highest frequencies and intensities of gull attacks on whales have been recorded. Similarly, the oblique breathing behavior could be observed from vessels that operate from Puerto Pirámides, but mainly in coastal sightings, probably due to the greater frequency and intensity of attacks near the coast (Fazio et al. 2012). Sightings with oblique breathing increased significantly in El Doradillo between 2012 and 2013. Moreover, oblique breathing frequency was similar between El Doradillo and Puerto Pirámides in 2012, but was significantly higher in El Doradillo in 2013, where higher attack rates were recorded. In the latter area, there is an important coastal flying corridor for gulls that fly to and from the dumps of Puerto Madryn city, which could increase the encounter probabilities between whales and gulls and then could increase the attack rates and the oblique breathing behavior. El Doradillo also has a higher number of whales, especially mother–calf pairs, which could favor the imitation of the oblique breathing behavior among whales.

The frequency of oblique breathing showed some changes along the season in El Doradillo between 2012 and 2013. In 2012, the oblique breathing frequency was higher in the first half of August, coincidentally with the higher frequency and intensity of gull attacks. Then, as the whale season progressed, both the oblique breathing behavior and the intensity of attacks proportionally decreased. However, in 2013, although the intensity of attacks was declining throughout the season in a similar way to 2012, the percentage of sightings with oblique breathing slightly increased. This could indicate some learning and imitation of the oblique breathing as a strategy to avoid the attacks in this area. Imitation is an advanced behavior whereby an animal observes and exactly replicates the behavior of another (Bouton 2007). Adults are not the only ones that could imitate the oblique breathing from other adults; calves are apparently learning this behavior as well by imitation of their mothers because they are displaying it from birth. Furthermore, adults breath obliquely even in the absence of attacks (Fig. 3), which could indicate that they are showing their calves how to breath obliquely or

Table 3 Description of the sightings where galleon position and/or oblique breathing was observed according to data obtained from different sampling periods and areas

Period	Area	Total no. of sightings	Focal whale category	No. of sightings	% sightings with galleon (*N*)	Description whales in galleon	% sightings with oblique b. (*N*)	Description whales in oblique b.
2009–2010	Dor	657	Other	91	0	–	0	–
			MC	566	5.1 (29)	Mothers	8.8 (50)	mothers and calves (no number data)
2012	Pir	486	Other	133	0	–	2.3 (3)	1 ♂ and 2 adults (undetermined sex)
			MC	353	3.1 (11)	Mothers	2.8 (10)	10 mothers and 5 calves
	Dor	396	Other	48	0	–	2.1 (1)	1 adult
			MC	348	3.7 (13)	Mothers	14.1 (49)	32 mothers and 37 calves (♀and ♂)
2013	Pir	355	Other	127	0	–	0	–
			MC	228	0.4 (1)	Mothers	13.6 (31)	1 mother and 30 calves (♀and ♂)
	Dor	447	Other	78	0	–	38.5 (30)	1 ♂ and 29 adults (undetermined sex)
			MC	369	0.8 (3)	Mothers	77 (284)	221 mothers and 158 calves (♀and ♂)

Solitary large females and most possibly pregnant because of the widened shape of the back

Galleon galleon position; *Oblique b.* oblique breathing; *MC* mother–calf pair; *Other* mating group or solitary individual; *Dor* Doradillo; *Pir* Puerto Pirámides

that mothers just display this behavior when they see a gull in order to prevent an attack. The establishment of the oblique breathing behavior could then have three different phases. In the first stage (from 2008 to 2010), the emergence of the oblique breathing behavior occurred; in a second stage (2012), this behavior is mainly a consequence of the stimulus (gull attacks); and in a final stage (2013), the whales breathe obliquely in a preventive way, even when attacks decrease. Nevertheless, it is important to consider that the observed decrease in attacks along the whale season could also be due to the effectiveness of oblique breathing as an antiparasitic strategy. In fact, in 2012 and 2013, between one to four percent of the gull pecks was recorded on whales' callosities over the head (the only exposed part of the body when performing oblique breathing), something rarely seen before. The latter could indicate that gulls are also changing their attack behavior in response to the oblique breathing. Another factor to consider is the three-year reproductive cycle of female southern right whales (Payne 1986). Adults present in the area in 2009 could have done oblique breathing or not because the behavior was just emerging, and then when they returned in 2012, they could have little experience in doing it. In contrast, cows in 2010 had probably more chances of breathing obliquely because the behavior was being learned, and then in 2013, when they returned to the area, they more probably had already learned this behavior. Therefore, some of the inter-annual differences recorded in oblique breathing may reflect different levels of prior experience.

The emergence of some whale postures in Península Valdés, such as the galleon position, to minimize the exposure to gull attacks was reported by Thomas (1988) together with the earliest records of gull attacks. We observed that the galleon position was only performed by adult female whales (both pregnant females and mothers with their calves) possibly because they stay longer in the area and remain longer at the surface nursing their calves in resting postures. On the other hand, adult males spend less time in these waters and do it in a more active way since their primary purpose is mating and then they would not be pressed to adopt those postures to avoid attacks. Calves have never been seen remaining in galleon position and therefore did not avoid gull harassment in this way. The oblique breathing, in turn, is used by all sex and age categories. In other reproductive areas of southern right whales where such attacks have not been reported, at least not directed to the back of the whale (South Africa, Australia and New Zealand), few seconds arching has been sporadically observed (J. Bannister, pers comm) but oblique breathing has not (P. B. Best, J. Bannister and E. Carroll, pers comm). Then, arching could be related not only to gull attacks, but also to resting or stretching behaviors, while oblique breathing seems to be only associated with attacks.

The oblique breathing behavior seems to be a useful way to reduce the exposure to gull attacks in the area of Península Valdés, and it took whales approximately 5 years to learn it. However, the performance of this behavior may entail extra costs. Studies made by Nowacek et al. (2001) showed that North Atlantic right whales are positively buoyant near the sea surface (several tens of meters depth)—whales use positive buoyancy to power glides during ascent. Therefore, oblique breathing could require extra energy expenditure because whales have to stay with the back and tail submerged against their natural buoyancy.

Recently born calves could be especially affected because their respiratory rates are twice as high as those of adults (in El Doradillo, the mean adult whale respiratory rate was 44 breaths h^{-1} and the one for calves was 97 breaths h^{-1}) and therefore also their number of oblique breaths. The stress that attacks may cause could have a direct effect on survival of calves in their first months of life and could contribute to the high mortality of calves of Península Valdés reported in recent years (Werner et al. 2011). Nevertheless, oblique breathing seems to be a useful strategy to prevent gull attacks.

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