

## Reciprocal Exchange and Subsequent Adoption of Calves by Two North Atlantic Right Whales (*Eubalaena glacialis*)

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### Abstract

Baleen whales have among the lowest reproductive rates in the animal kingdom, coupled with high energetic demands on lactating mothers to support the rapid growth of their offspring. Because each offspring represents a large portion of a female's reproductive effort, strong selection pressure should be in place to minimize the potential for misplaced parental effort. However, we describe a case in which two North Atlantic right whale (*Eubalaena glacialis*) offspring were switched between mothers and remained with their "adopted" mothers throughout their first year of life (until they were weaned). The most reasonable explanation is that this swap was an accident caused by the females calving in close spatial and temporal proximity. The calves likely associated with the wrong mothers before any mother-offspring recognition system had developed, and an association then formed between these non-biological mother-offspring pairs. These data raise intriguing questions regarding how often this may occur in other wildlife populations, what mechanisms are used for mother-offspring recognition in whales, and how long it takes for this recognition to develop.

**Key Words:** adoption, North Atlantic right whale, *Eubalaena glacialis*, mother-offspring recognition, parental care

### Introduction

Understanding the factors that influence strategies of parental care is a central theme of animal behaviour, evolutionary biology, and sociobiology (e.g., Alcock, 1998). Of particular interest are cases of adoption. These cases represent "Darwinian puzzles," wherein individuals expend resources in a manner that does not directly increase their

reproductive success (Alcock, 1998). Indeed, such behaviour could reduce the resources that individuals can contribute to raising their own offspring and, therefore, reduce overall reproductive success (Brown et al., 1995).

The evolutionary costs of misplaced parental effort should result in strong mechanisms for recognizing one's offspring and, therefore, minimize the chance of adoption. Many studies have now shown that two primary factors influence the rate at which mother-offspring recognition develops: (1) the potential interaction with the offspring of others and (2) the potential for mother-offspring separation. Species which give birth at high densities (where the probability of encountering offspring of others is high) or in situations where mother and offspring become separated develop mother-offspring recognition systems very quickly; whereas species that are solitary (where it is unlikely that parents will interact with an offspring that is not their own) or those in which mother-offspring dyads are not likely to be separated tend to develop these recognition systems more slowly, if at all (Klopfer, 1971; Beecher, 1982; Insley, 1992; Charrier et al., 2001).

The most thorough data available from wild cetaceans come from long-term studies of bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Australia. These dolphins are highly social and highly mobile and, thus, meet the above criteria facilitating selection for the rapid development of a mother-offspring recognition system. In this population, females prevent calves less than 1-wk-old from associating with other individuals, but such associations are allowed after the first week (Mann & Smuts, 1998). The authors suggest that this first week represents a "sensitive period" that is crucial for imprinting between the mother and offspring. Subsequent acoustical studies support this hypothesis, showing that the individual-specific "signature whistle" rate of the mothers

increases an order of magnitude once the calf is born, but returns to normal levels by the third week after birth (Fripp & Tyack, 2008). The hypothesis is that calves are imprinting on the mother's signature whistle during the first week, with the high whistle rate in the second week serving to solidify the calf's link between the mother and her whistle (Fripp & Tyack, 2008).

North Atlantic right whales (*Eubalaena glacialis*) are large baleen whales and have one of the lowest reproductive rates in the animal kingdom (Kraus et al., 2001) and, therefore, each offspring represents a large portion of a female's lifetime reproductive success. Moreover, each offspring represents an enormous energetic investment, with lactation lasting for ~1 y, for a large part of which the mothers themselves are fasting (Hamilton et al., 1995). The energetic demands of nursing a rapidly growing calf leave the mother with little blubber reserves, requiring at least one year of "resting" before she can become pregnant again (Kraus et al., 2001). Indeed, despite the vast size differences, whalers frequently obtained more oil from right whale calves than from their lactating mothers (Reeves & Mitchell, 1986).

Although the density of North Atlantic right whale females on their calving ground has never been quantified, females from multiple summer feeding grounds congregate on the calving grounds to give birth (Kraus et al., 1986a). Right whales in the southern hemisphere (*E. australis*) show similar migratory patterns and reach densities of ~100 mother-calf pairs/50 km<sup>2</sup>, indicating that densities can get quite high on the calving grounds. Moreover, these pairs tend to cluster together, resulting in high densities regardless of the amount of available area (Payne, 1986). Combined, the large investment females make in each offspring and this high potential for encountering other mothers suggest that strong mechanisms should be in place for mother-offspring recognition in right whales.

Long-term photo-identification and high-resolution genetic data (based on 35 microsatellite loci) were recently integrated for a comprehensive analysis of parentage in the North Atlantic right whale (Frasier et al., 2007). Briefly, maternity is assigned based on long-term associations between females and calves (Knowlton et al., 1994) and confirmed via genetic analyses, and paternity is assigned based on genetic analyses (Frasier et al., 2007). During this analysis, a case was found in 1987 in which the genetic profiles of two mother-calf pairs mismatched at several microsatellite loci, indicating that they were not consistent with their behaviourally determined mother-offspring relationships. Further analysis suggested that the calves had been switched

between the mothers. Although a sample mix-up or an error in one of the two databases would be the most parsimonious explanation, this situation represents a rare case for which there is particularly extensive photo-identification and genetic data that make it possible to rule out all potential sources of human error.

## Materials and Methods

Photo-identification data for North Atlantic right whales were collected primarily during ship-board and aerial surveys conducted throughout the known range (Brown et al., 2007). Photographs from opportunistic sightings and some research efforts go back as far as 1935, but uninterrupted studies began in 1980. Details of the photo-identification process are published elsewhere (Hamilton et al., 2007). Briefly, all incoming photographs are compared to identified whales in the North Atlantic right whale catalogue (Hamilton & Martin, 1999), and all photo-identifications are confirmed by one to two experienced matchers. All photo-identification analyses are conducted by eye, and matchers follow strict protocols to reduce the chance of errors (Hamilton et al., 2007). For the scenario found here, all photo-identification data were re-assessed and confirmed by four experienced matchers. Skin samples have been collected for genetic analyses since 1988 by several research teams, using a crossbow and modified bolt as described elsewhere (Frasier et al., 2009). Individual-specific genetic profiles are obtained for each sample based on the protocols described in Frasier et al. (2007). A recent comprehensive evaluation of the error rates in both the photo-identification and genetic data show that both of these methods provide reliable means of individual identification in right whales and have among the lowest error rates of any long-term study (Frasier et al., 2009).

## Results

All four of the whales involved have been genetically sampled multiple times (both mothers have each been sampled twice, one calf was sampled twice, and the other calf has been sampled three times), and the photo-identifications and genotypes for those events are consistent (Table 1). For the genotypes, the probability of two individuals having the same profile at the loci used is negligible, with the probability of obtaining two identical genetic profiles being  $5.92 \times 10^{-11}$  for two random individuals, and  $3.61 \times 10^{-5}$  for two siblings (Frasier et al., 2007). These consistent genotypes across multiple sampling events for each individual rule out potential errors in photo-identification, genetic

profiling, sample collection/labelling, and the links between whales and genetic profiles. This result is also confirmed by the fact that both calves in question are females and have since had calves of their own that have also been sampled: all photo-identification and genetic data are consistent with these additional mother-offspring relationships. If

**Table 1.** Photo-identification and genetic data for the two mother-calf pairs; included is the photo-identification and genetic data for the dates on which individuals were sampled and the sighting dates for the mother-calf pairs in 1987. Asterisks indicate sightings of the mother-calf pairs prior to when any identification of the calf could be made. Thus, the switch occurred on the calving ground prior to the 17 February 1987 sighting of 1004 and 1705, but it is not clear if the earlier sightings represent the correct or switched calves. Unambiguous photographic matches for the calves from their calf year to the year(s) they were genetically sampled are as follows: Whale 1705 – belly pigmentation from 17 February 1987 to photographs on 7 August 1996; whale 1707 – callosity pattern and lip ridge of 23 September 1987 match 1 September 1988 which match 27 August 1990 which match 4 August 1997.

Mother				
Mother photo-ID		Dates of sampling events	Genotype ID	
1004		27 Aug 1990	1004	
1004		16 Jan 1997	1004	
1151		22 Aug 2000	1151	
1151		22 Aug 2003	1151	
Calf				
Calf photo-ID		Dates of sampling events	Genotype ID	
1705		14 April 1993	1705	
1705		07 Aug 1996	1705	
1707		22 Aug 1990	1707	
1707		27 Aug 1990	1707	
1707		04 Aug 1997	1707	
Mother-calf assignment				
Photo-ID		Dates photographed in M-C association in 1987	Genotype ID	
Mother	Calf		Mother	Calf
1004	1705	Jan 1*, 14* & 15*; Feb 17; June 20; July 10; Sept 12, 13, 15 & 17; Oct 06	1004	1707
1151	1707	Feb 01*, Sept 23	1151	1705

an error had occurred in the photo-identification and/or genotype of the calves, then a mismatch would be expected between them and these subsequent offspring.

Neither calf was genetically sampled while associated with their purported mothers, so an error could have occurred in the photo-identification between their calf year and the year in which they were genetically sampled. Analysis by four experienced experts ruled out this potential source of error. In addition to using callosity patterns for these identifications (which is the common feature used to identify right whales [Kraus et al., 1986b]), photographs of ventral pigmentation (an unchangeable identifying feature of right whales [Kraus et al., 1986b]) were available for one calf and made it possible to confirm the identifications.

The photographic data show that the switch occurred on the calving ground by at least mid-February (Table 1). Both mother-calf pairs were seen during the winter months on the calving grounds off the coast of Georgia and Florida as well as during the autumn months on the feeding grounds in the Bay of Fundy. These data indicate that the mother-offspring associations were long-term and stable, probably lasting until weaning (*ca.* 11 mo), rather than spurious short-term interactions. Both pedigree and genetic data suggest that the mothers involved are not related, rejecting hypotheses of indirect fitness benefits via kin selection as potential explanations. Age and experience are known to affect a female's ability to successfully raise young, and inexperience has been suggested as the cause of adoption in polar bears (Derocher & Wiig, 1999). Although we do not know the ages of the mothers in this case, and have limited data on their early sighting histories, both appear to be relatively inexperienced mothers. One female has no known previous offspring, and the other has one known previous calf.

## Discussion

We suggest this swap was an accident caused by the females calving in close spatial and temporal proximity, with the calves associating with the wrong mothers before any mother-offspring recognition system had developed, and an association then forming between these non-biological mother-offspring pairs (Figure 1). Although this is the most realistic scenario, there are unfortunately little data available to provide more insight into the causes of this event. We do not know the specific day on which the calves were born, although one was seen on 1 January and was therefore obviously born prior to this date (and the other one was presumably born by then as well). Interestingly, on

10 December 1986, there was an intense storm off the coast of Jacksonville, Florida (in the middle of the calving grounds), during which wind speeds remained above 50 kts for 12 h. This would have resulted in surface turbulence, noise, and, thus, poor visual and acoustic conditions. The calving season starts in early December, and if this storm coincided with when the mothers were giving birth, it could have caused confusion between mothers and calves, hindered communication, and been a possible factor in facilitating this switch (Boness et al., 1992).

The ability to detect this event, as well as rule out any human errors as potential explanations, is due to the extensive and long-term nature of this study and the close collaboration between the photo-identification and genetic research teams. This sort of resolution is rare in studies of wildlife populations, and it supports the notion that pedigree analysis of wildlife populations provides an invaluable tool for understanding biological processes (Pemberton, 2008). These data also raise intriguing questions regarding how often adoption may occur in this and other wildlife populations, what mechanisms are used for mother-offspring recognition in whales, and how long it takes for this recognition to develop. Although a case of adoption was recently reported in a wild population of bottlenose dolphins (Howells et al.,

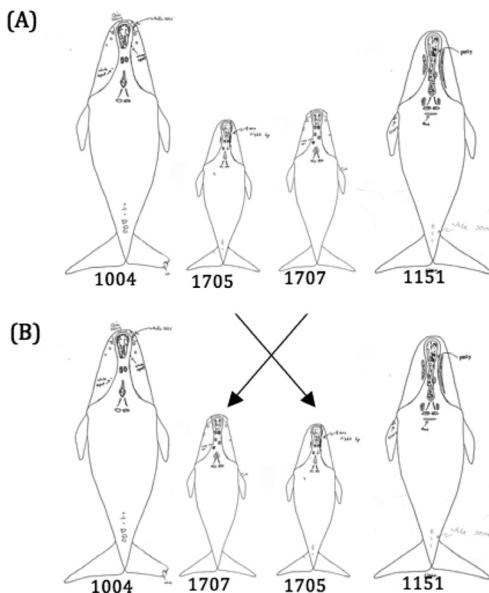
2009), this represents the first genetic confirmation of adoption in a wild cetacean, and the first documentation of adoption in a baleen whale.

Acoustic signatures are the most likely method of mother-offspring recognition in marine mammals. Indeed, pinnipeds use sound for this purpose despite having capable olfactory systems (Charrier et al., 2003). Although data are sparse for cetaceans, the first week after birth seems to be the key time for imprinting in bottlenose dolphins, a time when calves imprint on the mother's signature whistle (Mann & Smuts, 1998; Fripp & Tyack, 2008).

Right whales produce sounds ("up calls" or "contact calls") that may function as a means of individual identification. These are the only calls known to be made by newborn calves, their acoustic properties are well-suited for long-range communication, and they appear to be under selection to minimize overlap with ambient noise (Clark, 1982; Parks et al., 2007). Thus, these contact calls represent the most likely means of mother-offspring recognition in right whales. We hypothesize that these contact calls are the key feature right whale calves use to identify and imprint on their mothers, and that the two calves described here associated with the wrong mother prior to developing recognition of their mother's contact call. Imprinting then occurred between the non-biological mother-offspring pairs. This hypothesis leads to specific expectations regarding the properties and frequency of these contact calls. Similar to the situation with bottlenose dolphins, we expect there to be distinguishable differences between the contact calls of individuals, thus allowing a means of individual recognition. We also expect the rate of contact calls to greatly increase shortly after birth. Future analyses on the individual variation present in these calls, and their occurrence on the calving grounds, would shed much light on mother-offspring recognition in right whales as would analyses regarding whether or not right whale mothers actively avoid one another at the time of calving.

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**Figure 1.** Mother-calf relationships as determined through (A) photo-identification data and (B) genetic data; the numbers represent the individual identification number for each whale. Composite drawings are from the North Atlantic right whale catalog (Hamilton & Martin, 1999).

(www.rightwhaleweb.org). Funding for this work in particular was from the Canadian Whale Institute, National Marine Fisheries Service, Canadian Foundation for Innovation, the Natural Sciences and Engineering Research Council of Canada, and a Canadian Research Chair grant to Bradley N. White. The manuscript was greatly improved by the comments of Justin Gregg and two anonymous reviewers.

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