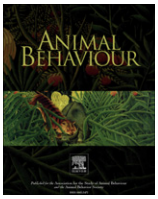
Animal Behaviour 82 (2011) 901–909

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



# Population-level lateralized feeding behaviour in North Atlantic humpback whales, *Megaptera novaeangliae*

Claire Canning[a,b,1], Danielle Crain[a,c,1], T. Scott Eaton, Jr[a,1], Kathryn Nuessly[a,1], Ari Friedlaender[c,*], Tom Hurst[d], Susan Parks[e], Colin Ware[f], David Wiley[g], Mason Weinrich[a]

[a] *The Whale Center of New England, Gloucester, MA, U.S.A.*
[b] *University of Exeter, Cornwall Campus, Penryn, Cornwall, U.K.*
[c] *Duke University Marine Laboratory, Beaufort, NC, U.S.A.*
[d] *Woods Hole Oceanographic Institution, Woods Hole, MA, U.S.A.*
[e] *Applied Research Laboratory, The Pennsylvania State University, State College, PA, U.S.A.*
[f] *Center for Coastal and Ocean Mapping, University of New Hampshire, Durham, NH, U.S.A.*
[g] *Stellwagen Bank National Marine Sanctuary, NOAA National Ocean Service, Scituate, MA, U.S.A.*

## ARTICLE INFO

*Article history:*
Received 1 May 2011
Initial acceptance 5 May 2011
Final acceptance 6 July 2011
Available online 17 August 2011
MS. number: A11-00353R

*Keywords:*
DTAG
feeding behaviour
handedness index
humpback whale
jaw scuffing
lateralized behaviour
*Megaptera novaeangliae*
North Atlantic

Lateralized behaviour refers to a preference for using a specific limb or direction of movement that is consistent across events. We investigated apparent lateralized behaviour in North Atlantic humpback whales, *Megaptera novaeangliae*, in the southern Gulf of Maine using digital acoustic tag ('DTAG') technology to analyse feeding behaviours during 2004–2009. An ideal tool to examine lateralized behaviours, DTAGs allowed continuous measurements of whale depth, heading, pitch and roll throughout the attachment period (less than 24 h). Side preference (right or left) in rolling behaviours (e.g. bottom rolling and side lunging) and directional preference (clockwise or anticlockwise) in feeding behaviours such as looping and spiraling were determined from visual examination of DTAG data. A 'handedness index' (HI) was used to quantify side bias and strength of preference. We found a population-level right-side bias similar to the 90/10 right-hand bias in humans. Furthermore, photos of jaw scuffing and direct tag data on rolling behaviour were used to assign a bottom-rolling side preference for 11 individuals for whom both of these data were available, 10 (90.9%) of which demonstrated a right-side bias. Consistent laterality was observed between individuals that performed bottom rolling and directional feeding behaviours, which was biased in the right/clockwise direction. Younger individuals tended to show weaker lateralization scores than older individuals, even among adults ($P = 0.048$), suggesting that lateralization develops, and continues to do so, beyond sexual maturity.

'Lateralization' refers to a particular preference for using a specific side of the body (e.g. a limb or direction of movement in mechanized behaviour, or a particular sensory organ such as an eye or ear) that is consistent across events. However, the origin of lateralized behaviour remains under debate. Denenberg (1981) states that individual preferences could be ontogenetic, suggesting that these preferences are learned and therefore lack evolutionary significance. For instance, immature chimpanzees, *Pan troglodytes*, show weaker laterality in hand use than adults, especially adult females (Humle & Matsuzawa 2009). However, Versace et al. (2007) demonstrated that lambs, *Ovis aries*, are more strongly lateralized in obstacle avoidance than adult sheep. Others suggest that in at least some cases laterality is driven by a similar neurological asymmetry across individuals in a population (McGrew & Marchant 1997; Rogers 2000).

Lateralization has evolved at both the individual and population levels. This behaviour has been commonly demonstrated at the individual level in various animal studies (i.e. side preference of trunk movements in Asian elephants, *Elephas maximus*: Haakonsson & Semple 2009; limb preference while performing routine daily tasks, such as locomotion, feeding, grooming and tool use, in several species of primates: McGrew & Marchant 1997; Peters & Rogers 2008). Lateralized behaviour at the population level may have evolved as an evolutionary stable strategy (Maynard Smith 1982) in order to coordinate behaviour using 'social constraints' among asymmetric individuals, providing higher fitness for the individual in the group (Vallortigara & Rogers 2005).

The most recognizable example of laterality at the population level is 'handedness' in humans, where approximately 90%

---

[*] Correspondence: A. Friedlaender, Duke University Marine Laboratory, 135 Pivers Island Rd, Beaufort, NC 28516, U.S.A.

*E-mail address:* asf7@duke.edu (A. Friedlaender).

[1] First four authors contributed equally to the manuscript.

0003-3472/$38.00 © 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2011.07.031

of individuals demonstrate a right-hand bias (Annett 1972). Population-level consistencies of lateralized behaviour are also apparent in nonhuman species (i.e. left-turn bias in the giant water bug, *Belostoma flumineum*, while swimming through a T-maze: Kight et al. 2008; right- pectoral-fin bias in the sound production of channel catfish, *Ictalurus punctatus*: Fine et al. 1996; right-side bias in obstacle avoidance in flocks of sheep: Versace et al. 2007; anticlockwise-circling bias in herds of free-ranging reindeer, *Rangifer tarandus*: Espmark & Kinderås 2002). Furthermore, a population-level right-sided preference for search and capture of prey has also been shown in teleost fish (Miklósi & Andrew 1999), lungfish (Lippolis et al. 2009), frogs and toads (Vallortigara et al. 1998; Robins & Rogers 2006), and birds (Ventolini et al. 2005; Rogers 2008).

Lateralization at the population level has also been well documented in numerous marine mammal species. Some of this information is derived from studies conducted in captive settings (e.g. studies of bottlenose dolphins, *Tursiops truncatus*, beluga whales, *Delphinapterus leucas*, and California sea lions, *Zalophus californianus*), although it is inherently limited due to constraints of both the setting and number of individuals studied (Sobel et al. 1994; Marino & Stowe 1997a,b; Wells et al. 2006). Lateralized behaviour in marine mammals has also been examined using scarring on carcasses of grey whales, *Eschrichtius robustus* (Kasuya & Rice 1970), photographs of scarring of live humpback whales, *Megaptera novaeangliae* (Clapham et al. 1995; Hain et al. 1995), and measurements of the density and length of pectoral appendages to determine limb bias based on increased mechanical stress in walruses, *Odobenus rosmarus*, and harbour porpoises, *Phocoena phocoena* (Levermann et al. 2003; Galatius 2005). In all of these cases, physical asymmetries were used as proxies to infer laterality with an overall bias towards the right side in the underlying behaviours. In North Atlantic humpback whales, 80% of individuals examined showed predominantly right side rostrum and mandible scarring, which was used as a proxy for laterality in subsurface feeding behaviours at the population level (Clapham et al. 1995). Surface behavioural observations, such as intentional beaching in the bottlenose dolphin (Hoese 1971), aerial displays (e.g. breaching, flipper slapping) in humpback whales (Clapham et al. 1995), and observations of wild beluga calf–mother interactions (Karenina et al. 2010) have also been used to determine population-level laterality in wild cetaceans. More recently, digital acoustic tag technology (Johnson & Tyack 2003) has been used to describe lateralized behaviour in feeding grey whales (Woodward & Winn 2006).

In this study we used photographic and tag-derived data to examine lateralization across a number of feeding behaviours in North Atlantic humpback whales in the southern Gulf of Maine. Humpback whales are large (12–16 m, 22 000–26 000 kg) baleen whales that typically spend their winters in low-latitude breeding grounds and their summers in higher-latitude feeding grounds (Clapham 2000). Feeding ground aggregations in this species appear to be maternally directed, with offspring mimicking the distribution of their mothers (Clapham et al. 1993). Prey for humpback whales in this area is primarily schooling fish including sand lance, *Ammodytes* spp. (Hain et al. 1982; Payne et al. 1990) and herring, *Clupea harengus* (Weinrich et al. 1997).

In the present study, (1) we examined whether scarring on the rostrum and mandibles of humpback whales could be used to infer the laterality of subsurface feeding behaviours, (2) we tested the hypothesis that humpback whales show consistent laterality within and between individuals, and (3) we examined whether the strength of laterality in feeding behaviours varies with age class.

## METHODS

### *Study Population*

Humpback whale fine-scale movement patterns and underwater behaviour were recorded using digital acoustic tags, or DTAGs (Johnson & Tyack 2003; Friedlaender et al. 2009). The DTAG is a noninvasive tag with four suction cup attachments points that is deployed from small inflatable rigid-hulled vessels. The tag is applied as the whale begins to dive, which results in a short-lived reaction, causing minimal disruption to the animals' activity. Tags are programmed to detach within 24 h and record an animal's heading, pitch, roll, acceleration and depth continuously using a sampling rate of 50 Hz. A VHF signal is emitted when the tag is at the surface to aid in its recovery. Data is archived on the tag and downloaded upon retrieval.

These tags have been successfully deployed on multiple species of baleen whales (Nowacek et al. 2003; Woodward & Winn 2006; Friedlaender et al. 2009). Whale tag data were collected under National Marine Fisheries Permits numbers 605-1607 and 605-1904 issued to The Whale Center of New England and Duke University Institutional Animal Care and Use Permit A041-09-02. During 2004–2009, 67 DTAGs were deployed on 57 individual humpback whales, resulting in over 456 h of on-animal data (10 whales were tagged multiple times). Five tag deployments were unusable for analysis (in one case the tag was not recovered; the remaining four fell off quickly); data for this analysis were therefore obtained from 52 individual humpback whales observed in 62 usable tag deployments (Table 1).

Tagged whales were categorized by age and sex class using the Whale Center of New England (WCNE) humpback whale catalogue in Gloucester, MA, U.S.A. Sex was determined by molecular techniques applied to biopsy samples (Baker et al. 1991; Berube & Palsbøll 1996), photographing males and females in the genital region (Glockner 1983), or previous observations of female individuals with a calf. In our sample of 52 individual tagged whales, 33 were female, 9 were male and 10 were of unknown sex. Age was determined either by seeing the animal initially as a young-of-the-year calf (exact age), the number of years since first sighted (minimum age), or seeing the whale with a calf (unknown age adult). Animals were classified as calves (<1 year), juveniles (1–4 years), subadults (5–8 years), adults (9+ years) and unknown (Sardi et al. 2005). Our sample consisted of 4 calves, 0 juveniles, 0 subadults, 43 adults and 5 whales of unknown age for which we calculated minimum age. This sampling bias is due to specifically targeting adults for tagging. Therefore, whales were split into categories by age. Category 1 included calves, category 2 included whales 1–8 years of age, category 3 included whales 9–16 years of age, category 4 included whales 17+ years of age, and category 5

**Table 1**
DTAG deployment information on the 62 humpback whales organized by year and location

| Year | Location | No. of whales tagged | Total tag time (h) |
|---|---|---|---|
| 2004 | GSC | 4 | 48:02:58 |
| 2005 | JL | 4 | 62:07:00 |
| 2006 | SB | 15 | 100:34:25 |
| 2007 | SB | 10 | 36:32:47 |
| 2008 | SB | 13 | 92:14:38 |
| 2009 | SB, JL | 16 | 116:52:28 |
|  | Total | 62 | 456:24:16 |

Total tag time for each year is provided. Locations include the Great South Channel (GSC), Jeffreys Ledge (JL) and Stellwagen Bank (SB). In 2009, whales were tagged in two locations: 9 in SB, 7 in JL.