Short Communication: Lateralised lunge-feeding behaviour in Southern Hemisphere fin whales at Antarctic feeding grounds

ALEXANDER NICOLAS RYCHWALSKI[1] AND HELENA HERR[2]

Contact email: alexander.rychwalski@gmail.com and helena.herr@uni-hamburg.de

ABSTRACT

Balaenopterids use dynamic feeding lunges to capture prey, often performing roll manoeuvres which may demonstrate a side preference or laterality. In this study, we use aerial video footage of fin whales (*Balaenoptera physalus*) feeding at Elephant Island, Antarctica, to investigate laterality in the Southern Hemisphere fin whale subspecies *B. p. quoyi*. Right-biased lateralisation was observed in all 63 recorded side lunges, 57 of which displayed visible lunge directions, the majority being clockwise (98.3%). These results complement existing information on lateralised feeding behaviour in Northern Hemisphere fin whales, confirming a strong right-sided bias across the different fin whale subspecies.

KEYWORDS: FEEDING; ANTARTIC; SOUTHERN OCEAN; FEEDING GROUNDS; BALAENOPTERIDAE; BALAENOPTERA PHYSALUS.

INTRODUCTION

Laterality or 'handedness' describes the asymmetrical left- or rightward inclination in the actions of individuals, which result in lateralised biases at a population level (Rogers, 1989). The origin of these lateral biases has been linked to asymmetric functions of the brain hemispheres regarding various stimuli and may have evolved in early vertebrates before the evolution of limbs (MacNeilage, 2013). Lateralised biases relating to hemispheric specialisation have been documented in the actions of a number of vertebrate groups, including fish, amphibians, reptiles, birds and mammals (Vallortigara & Rogers, 2005; Canning *et al*., 2011). Among mammals, lateralised behaviours during daily routine actions may have evolved as a stable strategy for coordinating behaviours between asymmetrical individuals within larger social settings and has been documented in several studies (MacNeilage, 2013; Vallortigara & Rogers, 2005; Canning *et al*., 2011; Ware *et al*., 2014). A well-known example of laterality at the population level is handedness in human beings, which is exhibited in 90% of the population possessing a right-hand preference and only 10% having a more dominant left hand (Rogers, 1989; Canning *et al*., 2011). Marine mammal populations in the wild exhibit side-biases during feeding-related activities, social interactions and asymmetrical limb usage (MacNeilage, 2013; Woodward & Winn, 2006; Karenina *et al*., 2016; Parks *et al*., 2014). This laterality is especially evident in cetaceans, which show signs of lateralised visual biases (sensory lateralisation) in social settings, such as mother-calf relations during nursing (Zoidis & Lomac-MacNair, 2017; Karenina *et al*., 2010), and also indicate 'handedness' (motor lateralisation) in their use of flippers (MacNeilage, 2013). The most pronounced lateral biases in cetaceans are exhibited during various foraging

[1] Universität Hamburg, Institute of Marine Ecosystem and Fishery Science, Große Elbstraße 133, 22767 Hamburg, Germany
[2] Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany

activities. These have been shown through direct behavioural observations and DTAG (Digital Acoustic Recording Tag) measurements (Jaakkola *et al*., 2020; Woodward & Winn, 2006), but are also evident through indirect feeding-related physical damage, such as jaw scuffing (Swingle *et al.*, 1993) and baleen wear (Kasuya & Rice, 1970). The observed foraging strategies which demonstrate a strong rightward lateralisation of around 90% range from beach feeding of *Tursiops truncates* (bottlenose dolphins; Silber & Fertl, 1995), feeding dives of *Megaptera novaeangliae* (humpback whales; Clapham *et al*., 1995; Canning *et al*., 2011) and *Eschrichtius robustus* (grey whales; Woodward & Winn, 2006) to surface lunge-feeding of several rorqual species belonging to the genus *Balaenoptera*, including *B. edeni* (Eden's whales; Chen *et al*., 2023), *B. musculus* (blue whales; Friedlaender *et al*., 2017; Friedlaender, 2022), *B. borealis* (sei whales; Tershy & Wiley, 1992), *B. brydei* (Bryde's whales; Tershy & Wiley, 1992) and *B. physalus* (fin whales; Tershy & Wiley, 1992). There are three recognised subspecies of fin whale (Pérez-Alvarez *et al*., 2021), two in the Northern Hemisphere *(B. p. physalus* and *B. p. velifera)* and one (*B. p. quoyi*) in the Southern Hemisphere, with a circumpolar distribution south of 20°S (Edwards *et al*., 2015). In the Northern Hemisphere, fin whales have been shown to display a strong right-biased lateralisation of ~90% during surface-feeding lunges (Tershy & Wiley, 1992), while information on foraging lateralisation has yet to be documented for Southern Hemisphere fin whales (SHFW). SHFWs are known to congregate at Antarctic feeding grounds during austral summers to forage on *Euphausiids* (krill) (Santora *et al*., 2014; Herr *et al*., 2022a; Viquerat *et al*., 2022), often forming large feeding aggregations involving up to 300 individuals (Herr *et al*., 2022a; 2022b). *B. physalus* possess an asymmetrically pigmented cephalic region, the left side being entirely dark slate and the right side being white on the ventral side and light grey in the dorsal cephalic area (Wursig *et al*., 2017). Distinctive anatomical features, such as this asymmetrically pigmented cephalic region, have been hypothesised to impact prey responses by acting as a startling device during prey herding or providing counter shading during feeding lunges (Tershy & Wiley, 1992). Here, we used aerial video footage to examine surface feeding behaviours of SHFWs at Antarctic feeding grounds to investigate lateralisation and directional lunging during feeding events.

METHODS & MATERIALS

The aerial video data of fin whale feeding events were recorded during the research expedition PS112 (Meyer & Wessels, 2018) of the German research ice breaker *Polarstern* (Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, 2017) to the Antarctic Peninsula from 18 March to 5 May 2018. The aerial footage was recorded during ship-based helicopter surveys (details in Herr *et al*., 2022a) using the on-board helicopter (BO-105), at an altitude of 600 ft (~183m), by a RED Helium 6K camera with Canon CN20 (50–1000mm) lens inside a GSS gyro-stabilised system as well as by drones DJI Phantom 4 and Inspire II equipped with a Zenmuse X5S camera, flown at an altitude of 100m. In total, 460 video files of SHFWs with a total duration of 3h 54min were recorded across 12 survey days within a period of 30 days at different locations around Elephant Island. Due to the relatively short flight times of around 15 minutes, the drones had to be frequently launched and retrieved, which resulted in each recorded video file being shorter than 10 minutes. Fin whales were encountered feeding in groups of one to 70 individuals (Herr *et al*., 2022a).

Feeding lunges were defined as the dynamic open-mouth pursuit and subsequent engulfment of prey, with those occurring in the upper ocean layer being referred to as surface feeding lunges. Lunge-feeding events were recorded as a single occurrence of a full-feeding lunge sequence performed by a single individual. Lunges exhibiting body rolls of less than 45° along the longitudinal axis were defined as straight lunges (ventral-side down). Feeding lunges displaying rolls of 45° or more to either side, occurring prior to the opening of the mouth and persisting in that position for the remainder of the active engulfment, were defined as side lunges (Canning *et al*., 2011; Woodward & Winn, 2006) and were classified in two categories, right-side lunges (RL) and left-side lunges (LL). Right-side lunges (> +45°) displayed a downward orientation of the right pectoral fin and vice versa for left-side lunges (< –45°). The assessment of body orientation during feeding lunges was performed by analysing the positioning of anatomical features, principally the buccal cavity and the appendages, as well as phenotypical characteristics, such as the white ventral region and the asymmetrically pigmented cephalic region (Wursig *et al*., 2017).

Lunge directions during side lunges were defined as straight, exhibiting no change in swimming direction, or as arced, exhibiting turning manoeuvres. These turning manoeuvres were recorded as either clockwise (CW) or counterclockwise (CCW) (Tershy & Wiley, 1992). The assessment of lunge direction was determined through the position of the lower jaw due to it always being located on the outside of the turning radius when the whales engaged in arced lunge directions (Fig. 1).

The proportion of arced lunge directions to either side, as well as lunges with no discernible change in direction, was expressed as a percentage of all lunging events. The degree of lateralisation during side lunges was calculated by dividing the difference of right- and leftward-directed rolls (> 45°) by the number of all observed side lunging events.

Lunge feeding events involving two or more whales performing simultaneous lunges (within a 10s timeframe), with a similar trajectory (same direction during lunge) and within close proximity to one another (one whale's length) were recorded as synchronised feeding events (Fig. 2).

The video footage was analysed with the programme QuickTime Player, using reduced playback speed of 0.5 (50% real time) as well as frame-by-frame processing. An accurate identification of distinctive features of individual fin whales using the video footage was not possible, therefore no examination of lateralisation on the individual level was performed. Instead, we used the observational count data from all side lunge events that were performed by fin whales feeding near the surface and visually analysed them for the proportion of side-rolling biases in order to investigate side preferences (Tershy & Wiley, 1992; Kot *et al*., 2014). Due to the lack of individual identification, we cannot confidently rule out that the same individuals were documented multiple times. However, due to the fact that filming took place over a duration of four weeks at multiple locations around Elephant Island and given the large number of whales present in feeding aggregations and captured in each drone recording, we assume our observations to be based on a diverse sample from a large population.

RESULTS & DISCUSSION

We identified 81 distinct surface lunging events, 63 (78%) of which were side lunges and 18 (22%) were straight lunging events. All observed side-lunge occurrences exhibited right-biased (RL) lateralisation (100%, n = 63). Lunge directions could be identified during 57 (70%) side lunging events, 56 of which (98.3%) exhibited arced, clockwise lunging (CW) and one (1.7%) displayed no directional lunging. We did not sample for prey, but echosounder records, as well as visual observations, indicated that *Euphausia superba* (Antarctic krill) was present in the study area (Meyer & Wessels, 2018). The presence of other krill predators, such as *Arctocephalus gazella* (Antarctic fur seals) and multiple species of birds, further indicated the availability of prey in the upper water column (Herr *et al*., 2022).

Our study found only right-biased lateralisation exhibited in the side lunges of fin whales during surface feeding events in the Antarctic. These results represent the first information on lateralisation in SHFWs and are analogous to findings from studies of the Northern Hemisphere subspecies, in which a strong lateralisation (> 90%) was documented during surface feeding lunges (Tershy & Wiley, 1992; Kot *et al*., 2014). Our analysis may therefore serve as a complementary commentary to Tershy & Wiley (1992), providing new information on lateralisation for the previously unstudied Southern Hemisphere subspecies, enabling a more comprehensive review of laterality in fin whales and the potential factors influencing it.

Rorquals exhibit remarkable levels of foraging efficiency that are approximately three to 10 times higher than those of some terrestrial carnivores and are needed to build up the large fat reserves needed for long migration and breeding periods (Potvin *et al*., 2021). Behavioural feeding strategies may therefore play an important role in regard to overall foraging efficiency as they offer a wide range of kinematic manoeuvres to react to dynamic prey fields and maximise engulfment (Goldbogen *et al*., 2015; Segre *et al*., 2019; Segre *et al*., 2022; Shadwick *et al*., 2019, Potvin *et al*., 2021). Prey density is considered a primary factor for behavioural adaptations during foraging and although complex lunge feeding manoeuvres (e.g., side rolls) require more energy to perform than straight lunges, they were found to be more frequently applied at less dense krill patches (Shadwick *et al*., 2019; Goldbogen *et al*., 2015; Cade *et al*., 2016). Krill have been shown to detect and avoid objects moving towards them by cohesively splitting up. This evasion strategy was successful for objects (nets, submersibles) travelling at about 1.0m/s but failed to be effective for speeds above 1.2m/s (Potvin *et al*., 2021). However, due to their enormous size, large rorquals are likely to be detected at greater distances, which would trigger the escape response of the prey earlier and afford them more time to disperse. Therefore, especially in larger individuals, higher lunge speeds and early detection avoidance (e.g., through manoeuvring or attacking from below) may be required to minimise krill dispersion and enhance engulfment success (Goldbogen *et al*., 2012; Potvin *et al*., 2021; Torres *et al*., 2020). Moreover, fin whales possess an asymmetrically pigmented cephalic region which has been hypothesised to function as a startling device during prey herding. This prey herding hypothesis suggests that whales predominantly employed clockwise or rightward swimming during lunge feeding to expose the white anterior region of their right side towards their prey to corral it into higher densities (Tershy & Wiley, 1992). Our observations of lunge directions exhibited an arced, clockwise direction during the majority of side lunges near the surface (98.3%), suggesting that SHFWs, particularly within the large feeding aggregations, may engage in prey herding to potentially reduce dispersion effects and improve foraging efficiency. This interpretation may be further substantiated by the large numbers of individuals (n = 35) which, aside from exhibiting signs of prey

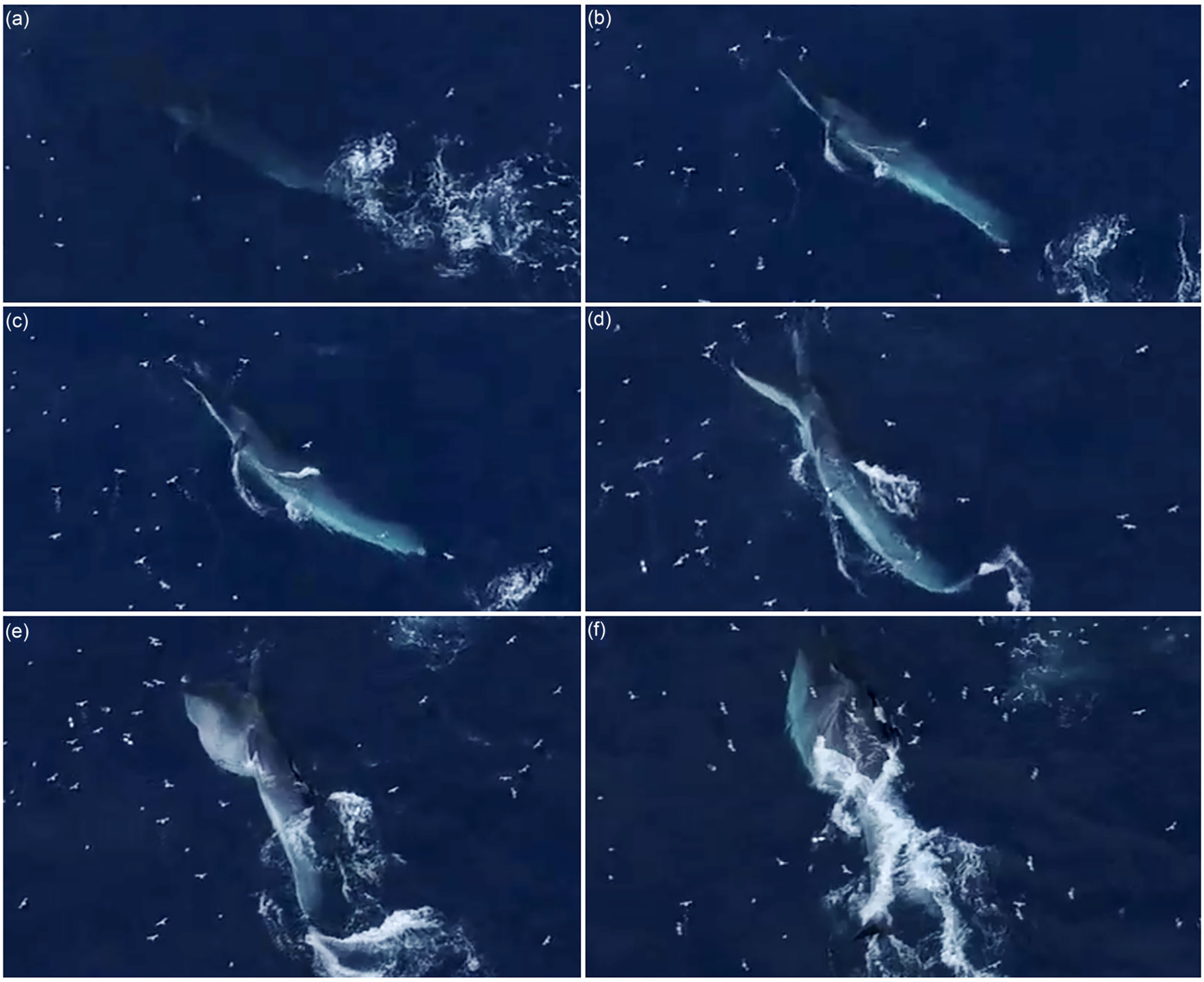

Fig. 1: Aerial photographs of an arced right-side lunge-feeding sequence performed by an individual fin whale: (a) lunge approach in upright position (ventral-side down); (b) initiating the side-roll manoeuvre along the longitudinal axis; (c) immediately before the start of the engulfment sequence, the side-roll position of approximately 90° to the right (right pectoral fin pointing down) is reached and the fluke is flexed upward (dorsally); (d) the engulfment sequence is initiated with the opening of the buccal cavity and the downward thrust of the fluke generating forward propulsion; (e) visible inflation of the ventral groove blubber (VGB) as the fluke is in the process of thrusting downward; (f) the end of the engulfment sequence, displayed by the closing of the buccal cavity while the VGB is inflated, as well as beginning to roll to an upright position while purging and filtering the engulfed water. Screengrabs obtained from video footage collected during RV *Polarstern* expedition PS112. ©BBC.

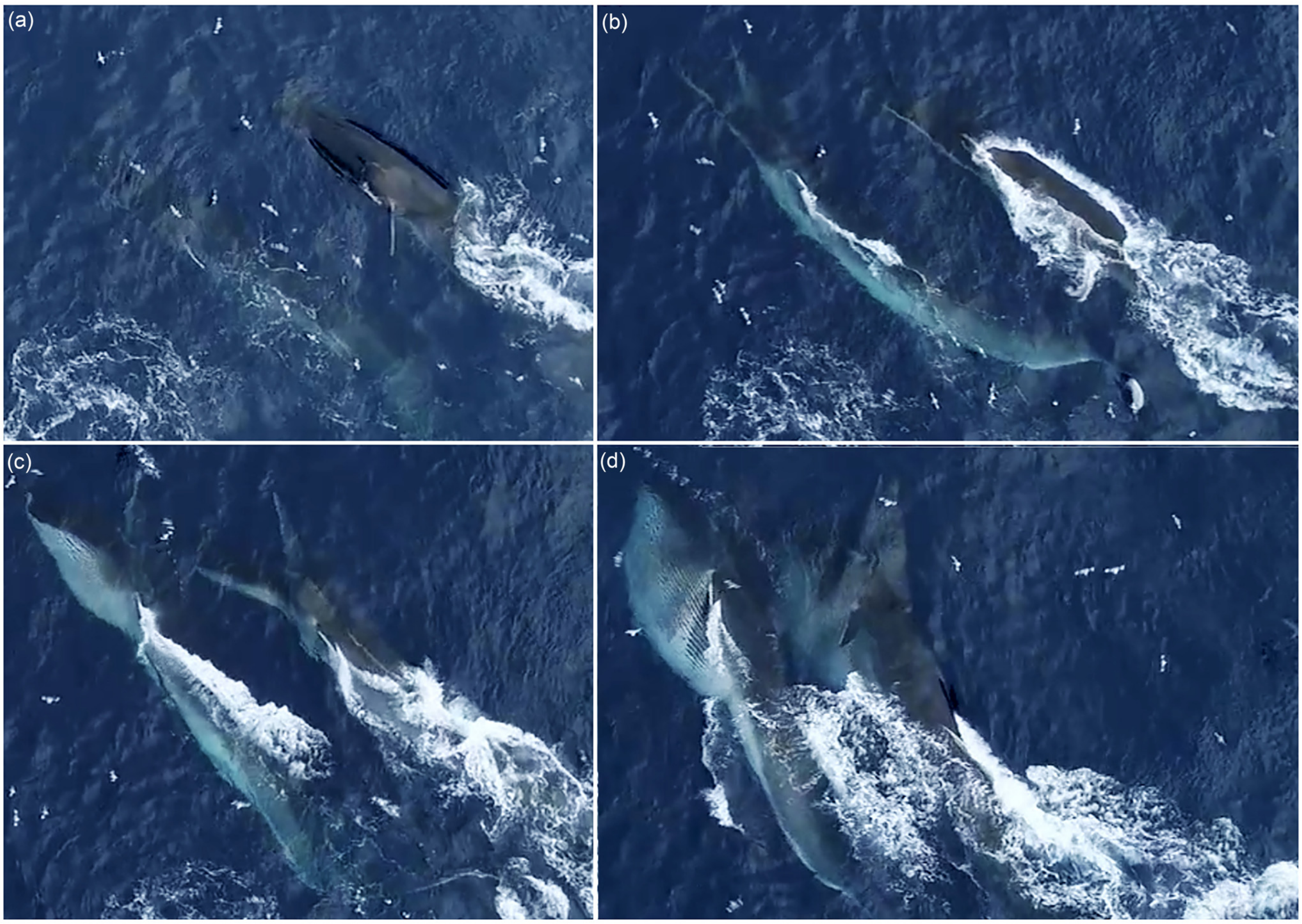

Fig. 2: Aerial photographs of a synchronised lunge-feeding sequence performed by two fin whales: (a) lunge approach in upright position (ventral-side down); (b) initiation of side-roll manoeuvres along the longitudinal axis; (c) active engulfment with a side-roll position of approximately 90° to the right (right pectoral fin pointing down); (d) the end of the engulfment sequence displayed by the closing of the buccal cavity and the inflation of the VGB. Screengrabs obtained from video footage collected during RV *Polarstern* expedition PS112. ©BBC.

herding, displayed synchronous feeding lunges involving multiple whales exclusively employing right side (RL) and straight lunges (SL) in close proximity to one another. Synchronised feeding of two to four whales (Fig. 2) occurred during approximately 40% of all recorded lunge feeding events and could be indicative of cooperative feeding behaviour, as described by Chen *et al*. (2023), in which the whales coordinated their approach and combined their engulfment capacities during feeding lunges. However, due to the small sample size of our observations this interpretation remains speculative and will require additional data collection and analysis.

In conclusion, SHFWs exhibited a strong degree of right-biased lateralisation during side lunge feeding, with predominantly right-biased roll manoeuvres and rightward (clockwise) lunge directions, which may be indicative of prey herding. These findings deviate from observations of Tershy & Wiley (1992), which, though displaying similarly high proportions of right-biased side lunges (97.4% in the Gulf of California and 81.1% in the Atlantic), only indicated a 52% side preference in lunge directions during feeding sequences, i.e., no prey herding. To further investigate if SHFWs engage in cooperative feeding strategies according to Chen *et al.* (2023), future research should investigate characteristics of synchronous and repetitive lunging behaviours involving multiple whales occurring within and outside the large feeding aggregations.

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