

ASYMMETRICAL PIGMENTATION IN THE FIN WHALE: A TEST OF TWO FEEDING RELATED HYPOTHESES

The fin whale (*Balaenoptera physalus*) is the only cetacean species and one of the few vertebrate species with consistent asymmetric body pigmentation. The left anterior third of the body and baleen are dark. The right anterior third of the body is less heavily pigmented, and the right lower jaw, including the mouth cavity and front baleen plates, is white (Mackintosh and Wheeler 1929, Tomilin 1957). The adaptive significance of this unusual pigmentation pattern has been the subject of considerable speculation. The pattern has generally been considered an adaptation for feeding and two non-mutually-exclusive hypotheses have been proposed. (1) The lateral lunge feeding hypothesis states that the function of asymmetrical pigmentation is to maintain counter shading when fin whales roll to their side during feeding lunges (Mitchell 1972, 1975). (2) The prey herding hypothesis suggests that the white anterior side of the head functions as a startle device, used to herd prey into higher concentrations (Mitchell 1975, Katona *et al.* 1983). We are not aware of any attempts to test these hypotheses, however they have been widely reported in technical and popular literature (Madsen and Herman 1980, Katona *et al.* 1983, Gambell 1985, Cousteau and Paccalet 1988). Here we provide a test of these two hypotheses using comparative data on lateral lunge preference in surface feeding for the fin whale, and four symmetrically pigmented congeners, the blue whale (*B. musculus*), sei whale (*B. borealis*), Bryde's whale (*B. edeni*), and minke whale (*B. acutorostrata*), in the Northern Hemisphere.

The lateral lunge feeding hypothesis predicts that fin whales lunge most frequently with their right (lighter) side down, and do so more frequently than their symmetrically pigmented congeners. The prey herding hypothesis predicts that fin whales herd prey, and do so by swimming in clockwise circles which would present the right side of the head towards prey.

Fin and blue whales were observed feeding on euphausiids, and Bryde's whales were observed feeding on schooling fish and euphausiids in the central Gulf of California, Mexico (113°20'W, 29°00'N), from May 1983–August 1986 (Tershy *et al.* 1990; Tershy 1992). Blue whales were also observed feeding on euphausiids in Monterey Bay, California, U.S.A. (121°50'W, 36°40'N) from October–November 1986 (Tershy *et al.*, *in litt.*).

Fin, sei and minke whales were observed feeding in the northwest Atlantic, during April–October, from 1985–1987. Prey were not identified, but sand lance (*Ammodytes americanus*), and capelin (*Mallotus villosus*) are important prey of fin and minke whales in the northwest Atlantic (Overholtz and Nicolas 1979, Whitehead and Carscadden 1985, Piatt *et al.* 1989, Payne *et al.* 1990), thus, we suspect that fin and minke whales were feeding on fish during some of the observed feeding events. Observations were made in the southern Gulf of Maine (42°17'N, 71°20'W), New York Bight (41°00'N, 71°00'W), and

the Gulf of Saint Lawrence, Canada (36°50'N, 64°00'W) (Wiley and Young 1987).

Whales were observed from vessels ranging from 5 to 26 m in length. Feeding was operationally defined as a lunge when the whale's open mandibles were visible above the water's surface. Thus we only recorded data on whales feeding on prey in the upper ~2 m of the water column. Lunges were recorded as right-side-down, left-side-down or non-lateral (dorsal or ventral surface down). Non-lateral lunges were not used in this analysis. Arc swimming was operationally defined as a curved surface movement pattern during feeding sequences. We frequently observed entire lunges, from the initial increase in speed before the mouth was open, until the mouth was closed, and did not see sudden changes in body orientation in the latter part of the lunge.

Arc swimming patterns were recorded as clockwise (occurring to the right) or counter-clockwise (occurring to the left). Data on arc swimming behavior was recorded for fin whales only.

Lateral lunges for fin whales were primarily right-side-down (Gulf of California 97.4%, $n = 304$; Atlantic 81.1%, $n = 212$). However, lateral lunges were also primarily right-side-down for the three largest symmetrically colored whales in the genus *Balaenoptera* (blue whale 100%, $n = 102$; sei 85.5%, $n = 62$; Bryde's 94.9%, $n = 137$; binomial probability test $P < 0.0025$ for all species). Only the minke whale, the smallest whale in the genus *Balaenoptera*, did not lunge significantly more often right-side-down (56.7%, $n = 30$; binomial probability test $P > 0.5$).

We did not observe obvious prey herding in any of the five species in the genus *Balaenoptera*. When whales were apparently feeding at depth, they frequently swam in a semicircular, circular or figure-eight pattern. Although we interpreted this swimming pattern as an attempt to remain above a localized prey patch, it is possible that they were prey herding. However, fin whales turned equally in both directions (52% clockwise, $n = 491$, binomial probability test $P > 0.5$).

Our data on surface feeding do not support the lateral lunge feeding hypothesis for the function of asymmetrical coloration in the fin whale. Although fin whales lunged most often with their right side down, so did their symmetrically colored congeners. Thus asymmetrical coloration is not uniquely associated with right-side-down lunging.

If asymmetrical pigmentation is a feeding related adaptation, it must now be explained why it has not evolved in other *Balaenoptera*. The diet of fin whales includes the euphausiids preyed on by the more planktivorous blue whales, and the fish preyed on by the more piscivorous Bryde's whale (Gaskin 1982). Thus, there appear to be no unique attributes of the prey that would select for asymmetrical coloration in the fin whale but not in either the blue or Bryde's whale. The non-adaptive scenario, that the mutation for asymmetrical pigmentation has only occurred in the fin whale, is not a testable hypothesis. However, it is interesting that asymmetrically colored individual sei and minke whales have been reported (Matthews 1978, Best 1985), yet these mutations have not led to fixation of asymmetrical coloration in either species.

The possibility that detailed observations of fin whales feeding below the surface could reveal markedly different behavior cannot be ruled out. However, from the vantage point of a 45-m cliff top B.R.T. recently observed a fin whale lunging below the surface and did not find qualitative differences from the surface feeding reported here.

The most parsimonious hypothesis may be that the right-side-down lunging preference observed in the four largest species is a by-product of the hemispheric laterality in the brain, the apparent cause of right forelimb preference in many mammals (Walker 1980). Differences between species are difficult to evaluate due to differences in prey type; however, they may be related to differences in body size (Wiley 1989; Tershy 1992; Tershy *et al.*, *in litt.*).

In conclusion, it should not be assumed that asymmetrical pigmentation in the fin whale is a feeding related adaptation. Other aspects of fin whale behavioral ecology should be investigated in relation to this unusual coloration and then tested by comparison with the symmetrically colored *Balaenoptera*.

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