

ZOOL 567 - Literature Review Assignment #3

Annotated Bibliography

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While the field of humpback whale song remains a relatively young area of study, it has grown significantly over the past few decades. This annotated bibliography is organized chronologically to specifically illustrate how our understanding of this behaviour has evolved and developed over time.

Payne, R. S., & McVay, S. (1971). Songs of humpback whales. *Science*, 173(3997), 585-597. <https://doi.org/10.1126/science.173.3997.585>

Summary: While many different species of whales are capable of vocalization, humpback whales (*Megaptera novaeangliae*) appear to produce highly complex vocalizations that follow specific patterns. Previous researchers had been largely unsuccessful in attempting to characterize the nature and structure of these sounds.

Payne and McVay (1971) reviewed hundreds of hours of archival humpback whale sounds in order to analyze the structures and patterns present among these vocalizations. This review primarily focused on two major repositories of humpback whale recordings. All recorded vocalizations were captured in known humpback whale breeding grounds over nearly two decades (1953 to 1971). Almost all of these recordings had also been subsequently transcribed into spectrographs, which illustrated the various sound wavelengths and patterns present across each recording.

Among these vocalizations, the authors were able to identify a series of varied, structured vocal patterns that were frequently repeated by individual humpback whales. These patterns were subsequently termed as “songs”. Songs were composed of specific sequential patterns and could be generally categorized, depending on the song’s predominant themes. Individual whales also appeared to be capable of producing unique song variations.

These findings are incredibly significant to the field of humpback whale research. Payne and McVay (1971) were the first to suggest that the unique vocal patterns of humpback whales be termed as songs, due to their repetitive and sequential nature. This terminology still persists in current research. Additionally, the characterization of specific whale song elements provides an essential framework for whale song analysis.

Payne and McVay (1971) suggest that future research into sex-specific vocalization among humpback whales may uncover physiological factors that contribute to variation in whale songs. They also acknowledge that the purpose of song among humpback whales is widely unknown - pair bonding, migrating, and mating are suggested as potential explanations.

Contribution: This article's analysis and review of recorded humpback whale songs provides groundbreaking insight into the structures and characteristics of these vocalizations. Previous research in this field failed to characterize humpback whale vocalizations as unique song patterns. The authors also highlight a number of follow-up questions that have since become fundamental areas of research in the field: determining the sex of vocalizing humpback whales and the specific function(s) of humpback whale song. Overall, this article's impact and relevance necessitate its inclusion in this literature review.

Winn, H. E., & Winn, L. K. (1978). The song of the humpback whale *Megaptera novaeangliae* in the West Indies. *Marine Biology*, 47(2), 97-114. <https://doi.org/10.1007/BF00395631>

Summary: Humpback whales (*Megaptera novaeangliae*) are known to produce relatively complex and patterned vocalizations. Previous research into these vocalizations has successfully managed to characterize common patterns and structures, but lacks insight into whether these songs differ from year to year. Winn and Winn (1978) analyzed the structure and patterns of humpback whale songs to determine the extent and nature of song variations.

The study consistently captured 8 years (1969 to 1977) of humpback whale recordings in a specific area of the Caribbean Sea. These recordings successfully collected 43 full-length humpback whale songs. Songs were captured with a hydrophone (a specialized underwater microphone) or a sonar recorder in close range during the humpback whale breeding season (January to April). The frequency of each recording was subsequently analysed and used to create a map of each captured song. Songs were further divided and categorized into six separate themes, with each theme representing a different structural component of the song.

Winn and Winn (1978) subsequently compared yearly variation across all six song themes and noted clear evidence of year-over-year variation between song themes. Song variation within any given year, however, was essentially non-existent, suggesting that yearly variations in song are incorporated in the spaces between breeding seasons. These findings are significant, as they represent the first documented instances of song evolution and suggest that humpback whales are capable of varying their song patterns.

The authors also identified potential opportunities for future studies focused on individual whales to confirm and clarify the nature of these yearly evolutions of humpback whale song. The existence of whale song 'dialects' may also be a possible area of study, as humpback whale breeding grounds and movement patterns are scattered throughout the Southern Hemisphere.

Contribution: The work of Winn and Winn (1978) provides novel insight into the nature of humpback whale song and how it varies from year to year. While previous research suggested that variation in whale song was a possibility, Winn and Winn (1978) were able to directly capture and characterize the nature of this variation. The authors also raise several interesting

questions for future research, particularly in the area of dialects and the nature of individual song variations. This article's key contributions to our understanding of humpback whale song necessitate its inclusion in this literature review.

Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology*, 8(2), 105-116.
<https://doi.org/10.1007/BF00300822>

Summary: Humpback whales (*Megaptera novaeangliae*) are capable of producing long and complex song patterns, and frequently engage in these vocalizations when they are in close proximity to their winter breeding grounds. While the capacity for song production is not unique to humpback whales, previous research has largely been unsuccessful in observing the interactions between singers and non-singers. Tyack (1981) observed the interactions between singing humpback whales and non-singing conspecifics to determine their nature and extent.

Tyack (1981) successfully observed 35 separate instances of actively singing humpback whales in their winter breeding grounds and tracked movement patterns for each whale using a theodolite. Theodolites are highly precise instruments that can be used to measure the distance and angles between multiple different points of observation. All of these whales were tracked and observed over the course of a single breeding season (February to March). Any conspecific interactions were recorded and subsequently analyzed.

From the 35 observed instances of humpback whale song, 22 whales completed their song with no conspecific interactions. 13 whales directly engaged in conspecific interactions, such as joining a larger group or a mother-calf dyad. All whales were observed as either stopping or pausing their singing prior to engaging in conspecific interaction(s). These findings are significant, as they support previous observational data suggesting that humpback whales prefer to sing alone, rather than in groups.

Tyack (1981) notes the need for additional studies into the overlap between humpback whale breeding seasons and the incidence of humpback whale song. While it is apparent that humpback whales generally prefer to perform solo song vocalizations, the songs themselves can still be heard over significant distances. The close proximity of singing whales to breeding grounds may also provide important insight into the potential purpose of humpback whale song in reproductive and breeding practices.

Contribution: This article characterizes the interactions that occur between singing humpback whales and conspecifics: humpback whales clearly prefer to perform songs individually and will cease singing prior to engaging in conspecific interactions. This supports previous research suggesting that humpback whales prefer to sing alone. Tyack (1981) raises several follow-up questions for future research that explore the potential role of humpback whale song in mating practices, based on the close proximity of humpback whale singers to their winter breeding

grounds. This article's contributions to the field and reinforcement of existing knowledge are key reasons for its inclusion in this literature review.

Tyack, P. (1983). Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds. *Behavioral Ecology and Sociobiology*, 13(1), 49–55. <https://doi.org/10.1007/BF00295075>

Summary: When male humpback whales (*Megaptera novaeangliae*) have successfully migrated to their winter breeding grounds, they frequently engage in long vocalization patterns, or songs. Previous research has suggested that interactions between singing humpback whales and non-singing whales involve the cessation of song, but it is unclear whether this cessation is directly related to the interaction itself. Tyack (1983) performed a number of playback experiments to determine whether humpback whales produce a different set of reactions in response to song vocalizations.

Tyack (1983) successfully performed 16 different playback experiments on small groups of humpback whales in winter breeding grounds. These playback experiments consisted of a recorded humpback whale song played in the vicinity of the humpback whale group, and close observation of their resulting behaviour. Playback experiments were subsequently repeated with recorded non-song vocalizations (social sounds) and the resultant humpback whale behaviour was observed.

In 14 of the 16 playback experiments using recorded humpback whale songs, humpback whale groups moved away from the source of the sound. This supports previous research suggesting that humpback whales prefer to sing alone, and that this preference is recognized by other whales in the breeding ground. Responses to social sounds were far more varied, with some groups of humpback whales actively charging the source of sound and others (namely cow-calf dyads) moving away from the source. These findings are very significant, as they suggest that different types of humpback whale vocalizations directly mediate avoidance or approach responses from conspecifics.

Tyack (1983) notes that additional studies are needed to specifically examine the responses of female humpback whales to song. Since most whales in the playback experiments were cow-calf dyads or groups of males, little is known about the specific female response to instances of humpback whale song.

Contribution: This article highlights key insights into how different humpback whale vocalizations can mediate responses from other humpback whales: songs are associated with avoidance, while social sounds can initiate approaches. This research emphasizes previous findings on the solo nature of humpback whale song and suggests that songs provoke unique behavioural responses in other whales. Tyack (1983) also highlights areas yet to be explored, including the nature of female humpback whale responses to songs. This article makes a

significant contribution to the field and provides important insight into mediated behavioural responses, making it an excellent article for this literature review.

Helweg, D. A., Frankel, A. S., Mobley, J. R., & Herman, L. M. (1992). Humpback whale song: Our current understanding. In J. A. Thomas, R. A. Kastelein, & A. Y. Supin (Eds.), *Marine Mammal Sensory Systems* (pp. 459–483). Springer US.
https://doi.org/10.1007/978-1-4615-3406-8_32

Summary: The presence and use of complex song vocalizations in humpback whales (*Megaptera novaeangliae*) is well-documented. However, the purpose of humpback whale song remains highly elusive. While previous research has resulted in a broad range of hypotheses, there is still no general consensus in the field.

Helweg et al. (1992) performed an extensive systematic review of existing literature on humpback whale song and vocalization (from 1945 to 1991). This review had two primary focuses: to compile a general description of the various methods used in whale research and to complete a comparative analysis of studies analyzing the overall purpose of humpback whale song.

The review found three primary methods for identifying and tracking whale behaviour: photographic identification, behavioural observation, and theodolite tracking. Photographic identification allows researchers to track individual whales via their unique tail fluke markings. Behavioural observation provides key insights into the timing, nature, and frequency of behaviours of interest. Finally, theodolite tracking involves the use of a specialized tool (a theodolite) to measure locations and positions of whales from a distance. Helweg et al. (1992) also noted that most studies tend to use a combination of two or more methods, depending on the desired outcome.

While the review's comparative analysis on the purpose of humpback whale song found no single conclusive explanation, Helweg et al. (1992) proposes that humpback whale song may actually serve numerous functions in humpback whales. This proposition is significant, as this is one of the first pieces of literature to suggest multiple, simultaneous functions of song in humpback whales. Some of these functions, like influence on mating rituals, are currently heavily studied. Other potential functions, such as the role of humpback whale song in migration, still require further research.

Contribution: This article's synthesis of common research methodologies and its comparative analysis of existing literature on humpback whale song offers a unique perspective into the purpose of these vocalizations that clearly advances the field. Proposing multiple, simultaneous functions for humpback whale song both supports existing literature and opens up additional areas of study beyond female choice and mate selection (e.g. migration and positioning). This

article's inclusion in the literature review is predicated on its contributions to the field and its synthesis of common methodologies in humpback whale song research.

Darling, J. D., & Bérubé, M. (2001). Interactions of singing humpback whales with other males. *Marine Mammal Science*, 17(3), 570-584. <https://doi.org/10.1111/j.1748-7692.2001.tb01005.x>

Summary: Male humpback whales (*Megaptera novaeangliae*) have frequently been observed to produce patterned, complex song vocalizations. Previous research hypothesizes that these songs may serve to attract female humpback whales, or that they may be part of a broader male-male competitive display. Darling and Bérubé (2001) analyzed the interactions of singing humpbacks and conspecifics to evaluate the validity of these proposed hypotheses.

The study captured 42 separate interactions between singing humpback whales and other males. These interactions were recorded using video and photo capture software. All audio recordings were captured using a hydrophone (a specialized underwater microphone). Whale interactions were recorded over the course of a single breeding season (January to April) and analyzed to determine potential behavioural patterns.

From the 42 observed interactions, 32 interactions (76%) involved a lone, non-singing adult male joining a singer. In the rest of the interactions, singers stopped vocalizing and proceeded to join other whales nearby. No female humpback whales were present in any of these groups, or involved in any interactions. The nature of the male-male interactions appeared to vary widely, with similar levels of agonist and non-agonistic behaviours observed. The presence of agonistic behaviours may suggest the presence of male social ordering or territorial displays. These findings directly contradict hypotheses on the role of song in female attraction, but suggest support for the role of song in a broader male-male competitive display.

Darling and Bérubé (2001) noted that additional observations were needed to confirm or refute the role of song in male-male competitive displays, as non-agonistic behaviours were still common among interacting males. Specifically, reviewing the comparative prevalence of agonist and non-agonistic behaviours between singing males may help further clarify the role of song in male-male competition and mating practices.

Contribution: This study forms the groundwork for future studies focused on the nature of male-male interactions. While previous research suggested humpback whale song may be implicated in female attraction, Darling and Bérubé (2001) found no supporting evidence for this hypothesis. The authors did, however, find evidence suggesting that song plays a role in male-male interactions. These findings require further examination into the dynamics of male-male interactions over multiple breeding seasons. Since this article builds significantly on previous research in the field and provides critical context for current insights into humpback whale song, it has been incorporated into this literature review.

Darling, J. D., Jones, M. E., & Nicklin, C. P. (2006). Humpback whale songs: Do they organize males during the breeding season? *Behaviour*, 143(9), 1051-1101.
<https://doi.org/10.1163/156853906778607381>

Summary: Male humpback whales (*Megaptera novaeangliae*) frequently produce long and complex song vocalizations during the winter breeding season. Previous research has failed to explicitly describe the various interactions that occur between singing males. Darling et al. (2006) captured and analyzed interactions between singers to determine whether any common male-male behavioural patterns emerged.

The study captured 167 separate interactions between singing males and conspecifics. These interactions were detected using a hydrophone (a specialized underwater microphone) and recorded using both video and photo capture software. Whales were recorded and tracked in a specific winter breeding ground over five breeding seasons (January 1997 through April 2002). Collected data was analyzed and reconstructed into full descriptions of behaviour, allowing the research team to identify both general and male-male behavioural patterns.

Of the 167 interactions observed, three major social groupings of singers were identified. 87% of singers were lone singers, aligning with existing research. In 149 (89%) of these interactions, singers immediately stopped vocalizing when they were joined by a non-singing male and both whales subsequently engaged in a brief interaction. The majority of these interactions were classified as non-agonistic in nature, with some interactions preceding additional communications with conspecific females. These findings are significant, as they appear to contradict previous hypotheses suggesting that humpback whale song may be directly involved in male-male competition or the communication of territorial boundaries.

Darling et al. (2006) noted that while the majority of observed male-male interactions were non-agonistic in nature, song may still serve to mediate behaviour and organize males during the breeding season. Additional research into the relationships between male humpback whales during the breeding season may help clarify the nature of these post-song interactions and center the role of song in humpback whale mating practices.

Contributions: Darling et al. (2006) provide critical insight into the nature of male-male interactions among humpback whales. Previous research in this field confirmed the solo nature of humpback whale song, but failed to sufficiently detail subsequent behavioural patterns among interacting conspecifics. The authors of this paper also raise key points for future research that emphasize further examination of male-male relationships across the breeding season. The article's novel insight into male-male interactions and contradiction of previous hypotheses make it a key piece of this literature review.

Herman, L. M., Pack, A. A., Spitz, S. S., Herman, E. Y. K., Rose, K., Hakala, S., & Deakos, M. H. (2013). Humpback whale song: Who sings? *Behavioral Ecology and Sociobiology*, 67(10), 1653-1663. <https://doi.org/10.1007/s00265-013-1576-8>

Summary: Male humpback whales (*Megaptera novaeangliae*) are capable of producing complex and highly structured songs. Previous research has failed to identify if these songs are exclusive to sexually mature humpback whales. Herman et al. (2013) analyzed the relationship between estimated sexual maturity and incidence of song among male humpback whales to determine if sexually immature humpback whales were also capable of song.

The study identified 87 male humpback whales that were capable of song and measured their body length using video capture software. These whales were recorded and tracked in an established winter breeding ground during the breeding season (January through April). This extensive tracking took place over a full decade (1998 to 2008). Historical whaling data was subsequently used to establish a relationship between humpback whale length and sexual maturity, allowing the research team to estimate the sexual maturity of each recorded whale.

Of the 87 humpback whales observed, 13 whales were classified as sexually immature. Each of these whales measured less than 11.3 meters (the length benchmark for sexual maturity). Based on their measurements, the probability of these whales being misclassified as sexually immature was low. These findings are significant, as they represent the first documented instances of sexually immature whales participating in song vocalizations.

Herman et al. (2013) also recognized the need for additional studies focused on the development of song in male humpback whales (including song components and structures). Identifying stages of sexual maturity and song development may help clarify when and how male humpback whales develop their vocalizations. The role of song is also a future area of study - it is unclear if song vocalizations are used by sexually immature whales as a tool to learn social cues and nuances associated with mating.

Contribution: This article provides new and important insight into the sexual maturity of male humpback whales engaging in song: both sexually mature and sexually immature humpback whales can sing. Previous research in this field was highly inconclusive about whether humpback whale song was exclusively limited to sexually mature males. Herman et al. (2013) also raise several follow-up questions for future research that focus on the evolution and role of humpback whale song across various stages of sexual maturity. The article's contributions to the field and suggestions for future research make it an excellent candidate for inclusion in this literature review.

Herman, L. M. (2017). The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: Review, evaluation, and synthesis. *Biological Reviews*, 92(3), 1795–1818. <https://doi.org/10.1111/brv.12309>

Summary: Male humpback whales (*Megaptera novaeangliae*) frequently produce highly complex song vocalizations. While the specific purposes of these songs are still unknown to researchers, previous studies have proposed several different hypotheses as potential explanations.

Herman (2017) conducted a highly extensive systematic review of articles focused on proposed functions of whale song (from 1937 to 2016). This review summarizes all currently known characteristics of humpback whale song and critically examines three major proposed functions of song vocalizations commonly referenced in the field of study.

The review provides the first comprehensive overview of all known characteristics of humpback whale song. Humpback whale song is exclusive to males and primarily produced in winter breeding grounds. Occasionally, vocalizing whales can also be observed along migratory routes. While singers typically prefer to perform solo, their songs range in frequency from 4-100 Hz and can be projected up to 10 kilometers underwater. Finally, these songs are highly complex, consisting of structured sequences of phrases, units, and themes.

The three major proposed functions of humpback whale song are as follows: female choice, mediation of male-male interactions, and the formation of a lekking system. Significantly, Herman (2017) notes that while the exact purpose of humpback whale song may still be elusive, it is clear that all three hypotheses are directly related to key aspects of mating in humpback whales, suggesting a base level of consensus among researchers. This level of insight represents a crucial milestone in the field of humpback whale song research.

Herman (2017) suggests that future research into humpback whale song should examine periods of oestrus or proestrus in humpback whales, in an effort to identify potential hormonal cues related to song production and responses. Herman (2017) also notes that evolutionary pressures on whale song should also be explored further, particularly within the context of migration.

Contribution: This article's synthesis of humpback whale song characteristics and its analysis of three major proposed song functions directly supports and provides critical insight into existing literature. No previous reviews have successfully characterized the themes and direction of the field's research, despite the availability of existing evidence. The author also highlights a number of follow-up questions to further examine potential proximal and ultimate influences on humpback whale song. Overall, this article's excellent synthesis of existing research and characterization of the field support its inclusion in this literature review.