

Literature Review 3: Annotated Bibliography  
ZOOL 567 - Animal Behavior  
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### ***Thematic Organization***

The thematic organization of the annotated bibliography follows the pattern of more general articles that narrow into more specific or context based studies. This allows for a smooth and comprehensive understanding of each study as one reads through the annotated bibliography.

### ***Annotated Bibliography***

Janik, V. M. (2009). Chapter 4: Acoustic communication in Delphinids. *Advances in the Study of Behavior*, 40, 123–157. [https://doi.org/10.1016/S0065-3454\(09\)40004-](https://doi.org/10.1016/S0065-3454(09)40004-)

### ***Article Summary***

Delphinids - a family of oceanic dolphins that includes the killer whale (*Orcinus orca*) - are shown to have a wide variety of different vocal signals that constitute their form of auditory communication. Auditory signals fall into three main categories: whistles, clicks and burst-pulsed signals that are used in short range echolocation, and long range communication calling. These sounds are assumed to originate from a sender that has sound producing apparatus in their nasal passage that can be received from a receiver's acoustic lens within their forehead. This allows all delphinids to communicate without opening their mouths and both put out and receive signals. Research on this type of signaling is predominantly a series of acoustic tags in specified areas that can pick up both long and short range calls, as well as tagging individuals within the same pods to study interactions of signalling. Types of calls are catalogued and individually specific calls are used to identify each delphinid due to their respective “auditory fingerprint”. Most study has shown that communication is taught down matrilineal lines through taught auditory learning that aid in foraging behaviour, nursing and maternal bonding, mating and movement within pod migration. Among species, dialects and call types change across geographic areas, and interactions between pods can lead to signal sharing that can be seen across similar species. Communication increased when auditory interference increased - seen by higher populated waters and human technology such as boats - and redundancy and types of signals change from situation and relative population around each pod for both community and individual signaling. Future research is projected to study signal cognition and neurological similarity of communication between taxa based on the study on communication found in delphinids that may show linkages of communication within how human language developed.

### ***Contribution and Significance***

This secondary source allows for the classification and identification of call types and research models used within the scope of orca vocalizations and the connections between how they evolved within the family of delphinids. This gives a general scope of where study has been historically, and where it should go to get the most cohesive image of how and why orcas communicate. Specifically for what this publication has contributed to the field, is the comparison between taxa and interspecies communication around killer whales, and why it is important with rising rates of anthropogenic action.

Reisinger, R. R., Beukes (née Janse van Rensburg), C., Hoelzel, A. R., & de Bruyn, P. J. N.

(2017). Kinship and association in a highly social apex predator population, killer whales at Marion Island. *Behavioral Ecology*, 28(3), 750–759.

<https://doi.org/10.1093/beheco/arx034>

#### *Article Summary*

Reisinger et al explores the bounds of kinship, and sociality in killer whales in the realms of vocalization, predation, morphology, movement, diet, and genetics. The Marion Island resident killer whales saw significant differences between both specialization of signalling, types of multimodal communication, predation tactics and events, as well as genetic variations and breeding interactions as individuals of one ecotype are sympatrically isolated from other clans and ecotypes. This gave way to limited to no interaction between residential orcas and transient or offshore orcas found near or migrating in close proximity to Marion Island. Reisinger et al takes a look at 20 residential whales in particular, aside from the comparative data collected from other studies on Marion Island orcas. Photographic identification was done in lieu of interaction counting between the 20 orcas to identify which individuals had the most stable relationships to their peers. What was found was that out of the subpod of 20 orcas, 8 social modules arose of 2-3 orcas each. An association index was conducted and discovered that the matrilineal units coincided with the respective social modules; the frequency of kin versus non-kin interactions were also mapped to show that association by age or sex was frequent in killer whales. This was confirmed through biopsy sampling of each of the killer whales and compared to one another with PCR amplified DNA to measure relatedness through genetic similarity. The relatedness of orcas in pods and their most stable and consistent associations show the most plausible sites for vocal interactions to occur, and for horizontal transmission to occur across individuals of the same generation rather than down the related matrilineal lineages. This specialization is thought to be motivated primarily by the predation advantage, as well specialization or generalization of an orcas diet compared to other ecotypes.

## *Contribution and Significance*

While not fully focused on orca vocalization, the relation to kinship and sociality to shifts in multiple components of orca specialization gives a cohesive look at how communication, signalling and behavior play a role in larger processes. Within this literature review, this article relates to the association of the orca vocalization as a socially dependent behaviour, and can give more insight of the contents for interactions to occur in which cultural transmission or information flow may occur. This can allow for further study in the dependence of other behaviours on vocalization, as well as how kinship events change vocalizations.

Riesch, R., Ford, J. K. B., & Thomsen, F. (2006). Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia. *Animal Behaviour*, 71(1), 79–91. <https://doi.org/10.1016/j.anbehav.2005.03.026>

## *Article Summary*

Identifying connections between groups of orcas can be done with different measures of similarities. Within this study, Riesch et al attempts to identify the similarity between stereotyped discrete calls and similarities between affiliate relationships between orcas within pods. This experiment follows 33 matrilineal lines composed of 216 individuals, that are a part of 4 clans that have distinct acoustic repertoires. The study of the dialectic similarity as well as conservation of similar sound across the 4 clans allows for us to understand how, why, and at what frequency familial association results in call sharing, and the blending of signature dialects. Whistles in killer whales are also not nearly as studied as burst-pulse or ‘call’ sounds, as it is very hard to distinguish the tonal shifts and differences in whistles across large populations of orcas, however they are extremely useful for orcas to use in close proximity and short range communication settings. Therefore, bioacoustic study focused on the similarity and exchanges of whistles amongs orcas can paint a clear picture of close individual based relationships. It was found the closely related clans - those that share or have closely associated groups of orcas - had the most similarity in generalized whistle calls. The more proximate interactions whales had, the closer their calls were both in structure and usage, and deviation correlates to how removed a matrilineal line is from a larger population using shared whistles. It was also observed that highly used and exchanged discrete whistling was more stable as a form of auditory communication then specialized ‘fingerprint’ whistles individual orcas produce, hinting that auditory learning happens not only down matrilineal lines, but horizontally across generations in similar pod structures.

## *Contribution and Significance*

The research done by Riesch et al is important to the entire study of bioacoustics in orcas, as the specific study of whistles in orcas was not very common at this point in time. This, in conjunction with the study of killer whales in close proximity to each other, is rare due to the preservation of non-invasive study of these highly influenceable marine predators. This form of innovative experimentation that follows all ethics standards within marine mammal observation allowed for a cohesive image to be formed about the base knowledge of overall killer whale vocal signalling, and associated social relationships.

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, 69(6), 1454–1483.

<https://doi.org/10.1139/z91-206>

### *Article Summary*

Prior to the series of papers published by Ford, there was little known about the types of dialects and grouping of vocalizations that are specific to orca pods. Orcas as a study organism are ideal for exploration as the population off the coast of British Columbia has been studied since the 1970s and are made up of around 70% resident killer whales that stay within the same vicinity most of their lives. In this study, Ford seeks to identify if there is a pod specific dialect in discrete calls, and to what extent they are shared across matrilineal lines all the way to communities. This is done to determine if there is proof of an ancestral pod that deviated all common vocalization types. Within this experiment, 16 residential pods comprised of 232 orcas were studied. Of the 16 pods, 13 make up the northern resident orca community and do not interact with the 3 pods found in the southern community. Photographs and acoustic recordings were done over the course of 154 days between June – September, reporting 426 pod encounters and identified calls that were classified and quantified into spectrographs. Acoustic recordings were then compared against each other and 43 prior recordings from a study in 1973 on Orca auditory behavior. It was found that most discrete calls were shared by several pods that interacted in one community. The frequency and type of calls however are sustained down generations as shown by the comparison of calls from the 1973 acoustic study. Pods that are isolated showed low signs of dialect sharing and had greater variations than other pods who had dialectic sharing. This shows that vocal learning is passed down matrilineal groups and sub pods so readily that similarities arise across pods that are most in contact.

### *Contribution and Significance*

Cited by 295 papers, studies conducted by Ford on Orca social dynamics and Ford's method of acoustic study in Orca vocalization is now intrinsic to marine behavioral study and research methodology for dialects in marine mammals. The ability to study aquatic vocal traditions are vital in the study of overall animal behavior and signalling and dialects are incredibly rare in terrestrial animals and mammals. The presence of taught signalling, and the ability to have isolation of communities seen in orcas shed important light on the overall study of animal communication and vocal signalling in relation to social species.

Miller, P. (2002). Mixed-directionality of killer whale stereotyped calls: A direction of movement cue? *Behavioral Ecology and Sociobiology*, 52(3), 262–270.

<https://doi.org/10.1007/s00265-002-0508-9>

### *Article Summary*

The physical production of sound by killer whales is a necessity to further study their most prominent form of vocal communication. Sounds produced by mammals are often non-uniform by design. The use of loud, omni-directional signals are used for instances such as territoriality, general signalling, or for calls that are not putting the signaller at a disadvantage if it is intercepted. This contrasts the form of signal 'beaming' that Miller studies in softer or fainter auditory signalling which convey alternate and more private information that is specific to a single or few receivers. Miller proposes that directional 'cueing' is the driving force behind the multifaceted form of identification signalling that orcas use while actively moving as a group or hunting. Signals that are amplified towards a certain direction can be interpreted by orcas familiar with multi-directional calling and can locate where the signaller may be, as well as being able to decode the physical message of the signal. Miller accredits the development of this type of signalling to gain the most efficient form of communication for the energy cost of vocalization. This was found by collecting calls and measuring radiation of calls at differing angles of mobile orcas in the A5 and W3 pods in British Columbia resident killer whales. Over 666 individual calls were compiled and sorted through for this analysis where radiation of sound, and energy projection in relation to sound waves were measured against frequency. This brings to light the discovery of mixed-directionality in auditory signalling, and that vocalizations are much more highly specialized and variable than initially thought by researchers such as Ford and Riesch.

### *Contribution and Significance*

The mapping and measuring of directionality in calls pulls attention to the use of honest versus dishonest signalling, and context based calling in orcas that can give more than one source of information at a time. This is significant in how communication is perceived and studied in

both marine signalling and in this literature review. Future research can now use Miller's study as a jumping point in how directionality and multimodal signalling play a part in taught signalling within orcas, and how this type of signalling may also be applied to visual signals and other forms of communication.

Samarra, F. I. P. (2015). Variations in killer whale food-associated calls produced during different prey behavioural contexts. *Behavioural Processes*, 116, 33–42.

<https://doi.org/10.1016/j.beproc.2015.04.013>

### *Article Summary*

While both whistle and burst-pulse calls are highly observed in orcas, situational based calls allow for a greater depth of understanding regarding frequency, type, and association of calls to specific groups of orcas and their behaviours. Samarra uses this experiment to determine calls specific to hunting and predation in killer whales to not only observe orca behaviour in hunting situations, but the shift and specialization of call types overtime. This experiment follows pods in Iceland, creating a specialized herding call in response to herring (*Clupea harengus*), a type of fish that travel in large groups - or school, within feeding locations. This call is specific to the Icelandic killer whales, and the frequency of herding calls are seen to increase the higher the population of herring. This organized call type was also associated with a specialized hunting behavior - herding of multiple orcas around schools of herring before striking a fish with a tail fluke to kill or disable it for feeding. This call is also observed temporally - increasing frequency in spawning flashes of fish the orcas feed on consistently, which shows how highly specialized and instructive feeding calls can be. 354 herding calls were analyzed with both auditory and video recording to see the frequency of the hunting event following the identified herding call - of which, was greater than 81%. This was observed over a five year period in two distinct pods of orcas. This food-based call allows for the study of specialization in vocal calls to change from different predatory behaviours, as well as the identification of an orca's feeding and transportation type (specialized or generalized; resident or transient), which in the case of this experiment, gives lots of insight on the overall pod dynamic of the icelandic killer whales.

### *Contribution and Significance*

The determination of vocal signals relating directly to an observed behavior is incredibly valuable on how much effect and how efficient vocal signalling is to social predators such as killer whales. The study of situational vocal signals allows for behavioural scientists to further study how language and vocal signalling affects animal behaviour, and how taught vocalization

is passed down in multiple different organisms and settings. Samarra's study shows the relation to specialization of call types to specific behaviours, as well as association of vocal development in different situations despite not being an initially learned signal.

Miller, P. J. O., & Bain, D. E. (2000). Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Animal Behaviour*, 60(5), 617–628.

<https://doi.org/10.1006/anbe.2000.1503>

### *Article Summary*

While other studies focus on the categorization and identification of variations in discrete calls, Miller and Bain 2000 seek to discover exactly how variations in calls arise, and why it's significant to the social structure of killer whales. Miller was the first to postulate that drift within calls is due to the splitting of matrilineal groups and fracturing of stable associations of orcas. Miller was also a key in furthering the idea of an epiphenomenon, or secondary mode of action, that can be used to measure pod stability - which is call sharing in larger groups of orcas such as pods or clans. While disproven in later studies - namely the many publications by Filatova and team - by what is now commonly referred to as the call repertoire of an orca, as well as the specific dialect an orca or a small association of orcas may have, and horizontal cultural transmission. Miller & Bain 2000 was and still is a foundational paper hypothesizing what proximate and ultimate motivations for call type change across orcas may be. These findings were made through the analysis and collection of 1784 individual calls over the span of 18 hours of active recording. Calls were then cross referenced to other databases of calls such as the one created by Ford in his 1991 study, and categorized based on call structure. This was then connected to specific matrilineal units in the study group of resident killer whales through the database as well as photographic documentation when calls were recorded. This was done to further measure the call usage rate of specific calls, and to determine difference and division based on 'fracturing' of calls based on each matrilineal unit. What was observed was clear deviation of calls between each matrilineal unit.

### *Contribution and Significance*

While slightly underdeveloped to what is currently known about orca communication, Miller and Bain 2000 was an integral publication when understanding both where research on orca vocalization started, as well as what the original assumptions and hypotheses were when marine behaviour was first being documented and compounded into large networks. For the scope of this literature review, the basal understanding of how deviation in calls and what lead to

the discovery of dialects later on is vital to the foundation of study - in both context and study methodology - to marine bioacoustics in delphinids.

Miller, P. J. O., Shapiro, A. D., Tyack, P. L., & Solow, A. R. (2004). Call-type matching in

vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. *Animal*

*Behaviour*, 67(6), 1099–1107. <https://doi.org/10.1016/j.anbehav.2003.06.017>

### *Article Summary*

Within this study, Miller et al looks at the distinguishable methods of vocal signalling in matrilineal lines with both call matching, percent vocal response, and directionality to measure interception of intended signal. This is highly significant due to the study method - the use of hydrophones and quiet-tracking vessels to more accurately capture signal interactions between individuals. This further develops what is known about the vocal exchange rather than just the singular event of calling or receiving within vocalization. The addition of directionality into this study gave way to a more comprehensive and cohesive killer whale call repertoire, as well as a further streamlined study method that was integrated into the field of marine bioacoustics. This very well takes the findings from Miller 2000 pulls the idea of interaction based call-matching to fully understand the environment in which orcas communicate and how it is done so efficiently. Using the comparison method founded by Ford to cross reference a vocal call with visual documentation, the hydrophone collected upwards of 274 minutes worth of active footage and recording of orca interactions, through 31 focal follows on isolated matrilineal units while mobile. Both stereotyped and varied calls were recorded and analysed to find that the usage of sequential calls that were either stereotyped or varied resulted in a higher response than single trill or truncated calls. In association to the focal vocal exchanges studied in this experiment, the mobile sequences of calls were compared against different matrilineal units to measure similarity, and found that differentiation between call types with vocal exchanges are very ranged and difficult to map relationships within this context. This lack of distinction between mobile call sequences is thought to support cultural transmission within more generalized pod dynamics.

### *Contribution and Significance*

While not an article that can contribute much to the discussion of dialect within taught orca language, the contextualization of call and respond based interactions within orcas for bioacoustic study is new not only in this field of research, but within the scope of this literature review and how call response is organized in orcas. This also brings light to the question of how modulation of social behaviour expresses itself in orca vocalization, and the depth of vocalizations can be studied in more social settings in the future.



Filatova, O. A., Deecke, V. B., Ford, J. K. B., Matkin, C. O., Barrett-Lennard, L. G., Guzeev, M. A., Burdin, A. M., & Hoyt, E. (2012). Call diversity in the North Pacific killer whale populations: Implications for dialect evolution and population history. *Animal Behaviour*, 83(3), 595–603. <https://doi.org/10.1016/j.anbehav.2011.12.013>

### *Article Summary*

Filatova et al takes a comprehensive look at cross-population comparison between the most studied orca associations present in research. Dialectic research to this magnitude is highly complex, as the geographic separation between the four populations that are studied in this experiment - resident killer whales from the North Pacific Ocean, both the Northern and Southern British Columbia and Washington state clans, Eastern Kamchatka, and Southern Alaska - are highly isolated from one another and do not migrate to great lengths unlike transient killer whales. Filatova et al looks at both monophonic (singular pitch transmission signals) and biphonic (dual pitch transmission signals) in orcas to determine just what distinction of call types exist between each population. Sound recording compiled through prior experimentation from 1980 to 2009 was compiled and analyzed alongside the environmental settings and identifiers used to collect initial data. This then resulted in the classification of calls that showed major variants down to the subgroup level. Here, Filatova et al looks at call similarity, structure, directionality, and call usage frequency to map the differences and similarities of all mentioned populations. It was found that both monophonic and biphonic calls from all four study populations were greatly varied, more similarity within the less used biphonic calls were found across populations compared to the highly varied monophonic calls. This not only supports the dialectic hypothesis, but change of call types through horizontal transmission. This also hints at an originating baseline call repertoire in which biphonic and monophonic signals must have originated from - most likely a matrilineal group that split and segregated over time into the isolated clans we see now, and resulted in separate, divergent specializations of taught learning.

### *Contribution and Significance*

While being co-written by major members of the orca bioacoustics community, all concepts from Ford, Riebel, and Miller's foundational papers were integrated and mentioned throughout this article. The information discovered from this paper helped solidify how transmission of learned language in orcas is highly variable to an individual's environment and requirements of communication - such as diet, and predation. Within this literature study, this creates a cohesive look on what the consensus of understanding is surrounding orca vocalization as it is consumed now, as well as the ultimate influence on where orca vocalization arose from.

Riesch, R., & Deecke, V. B. (2011). Whistle communication in mammal-eating killer whales (*Orcinus orca*): Further evidence for acoustic divergence between ecotypes. *Behavioral Ecology and Sociobiology*, 65(7), 1377–1387.  
<https://doi.org/10.1007/s00265-011-1148-8>

### *Article Summary*

Riesch and Deecke observe the mechanisms and motivations behind private versus public calling in orcas, and the contexts they arise in. Within this study, researchers look at both stereotyped calls - or easily identified monophonic acoustic signals - and variable calls - that are made up of sequential, train, or biphonic acoustic signals that are harder to identify. The use of public, or very widely dispersed calls are assumed to be for mating, territorial, and possible threat displays within orcas, whereas the private, or short range signals are assumed for translocation of prey, and others associated with a hunting party. Riesch and Deecke looked at short range whistle calls that range upwards to the ultrasonic range in both resident and transient whales. 1218 whistles were found within the bioacoustic preamters set within the study design and analysis to see how many were varied, and how many were stereotyped in transient whales and then compared to get a baseline of whistle usage in both ecotypes. This experiment looked at the 50 hour worth of West coast transient killer whales to create a baseline of data for frequency of whistles produced. It was found that 42% of all transient whale stereotyped whistles were isolated and in public range. This contrasts the data collected for the resident whales from auxiliary research studies that showed that 50% of all whistles are signatures within resident killer whale vocal exchanges. This shows that the use of context based, heavily developed specialized call repertoires are more likely to occur with transient whales due to their heavily specialized diet and migration status. Whereas the resident whales have a wide, diverse call repertoire to fit their ecotype's environment.

### *Contribution and Significance*

The presence of separation based on ecotype - between transient and residential whales - is not common to see in study and the addition to this literature review gives a greater understanding for the development of specialization of calls, and how they may be used in both a stereotyped and variable context. The introduction of transient orca vocal exchange brings up the interesting question of where and how cultural transmission occurs in this specific ecotype, and how the distinction of vocalization started between ecotypes from an evolutionary perspective.