

## ZOOL 567 – Annotated Bibliography

The first source contains an overall context of wolf howling behaviour. The next source was the earliest paper I could find on my topic, with each additional article building off the information from the last.

**Harrington, F. H., & Asa, C. S. (2003). Wolf communication. In L. D. Mech and L. Boitani (Eds.), *Wolves: Behaviour, ecology, and conservation* (pp.66-103). University of Chicago Press.**

**Summary:** Previous work has found that wolves are very social animals and that much of their social interactions are accompanied by vocalizations. In this book chapter, authors sought to examine what signals wolves use to communicate and determine what messages they include. Harrington & Asa (2003) used literature up to the year 2000 that included different types of studies, to determine how vocalizations develop in wolves and what each type of vocalization is used for. This work synthesizes how howling is used by solitary wolves and wolves in packs as a form of auditory communication over extended distances. The authors found that chorus howls (vocalizations made by packs of wolves) can be “harmonious” (small variation in pitch between wolves) or “discordant” (random variation in howl pitch and energy between wolves). The type of chorus howling used may be impacted by how close packmates are to each other, however, further research is required due to contradicting results from other studies. Since single wolves don’t have the safety of being with packmates, they howl more softly compared to chorus howls, so they are less likely to be detected by strangers. Howls serve to “coordinate movements” between dispersed wolves belonging to the same pack, intensify social relationships between packmates, help to stay away from other packs, and help solitary wolves find mates. This suggests that howls have inter- and intra-pack functions in communication. This work allows us to understand what information is included in a wolf howl, giving us more insight into their language. The authors suggest that future studies are needed to determine how variation in howls between individuals allows wolves to identify one another, as well as how the frequency of howling between individuals results in differences in social cohesion within packs.

**Contribution:** This book chapter is included in my literature review because it summarizes the social factors that influence wolf howling behaviour, providing an in-depth overview of the howl characteristics and in what social contexts howling is used. This work synthesizes inter- and intra-pack functions of howling and provides evidence from other references to support the social functions of howling. While this book chapter supports the findings of many articles, it also highlights where some articles contradict each other, and where further research is needed, such as how location relative to packmates may or may not affect the arrangement of chorus howls.

Theberge, J. B., & Falls, J. B. (1967). Howling as a means of communication in timber wolves. *American Zoologist*, 7(2), 331–338. <https://doi.org/10.1093/icb/7.2.331>

**Summary:** Previous work has shown that howling is frequently used by members of the genus *Canis* to interact and is one of many vocalizations made by wolves. This study aimed to investigate if variation in howls could be detected by wolves and what those variations mean. Over the summers of 1964 and 1965, Theberge & Falls (1967) used three captive wolves and placed them in pens located 3.5 miles and 0.25 miles away from the main pen at the Wildlife Research Station in Ontario. The further pen ensured that wolves would not be able to see or hear their packmates in the main pen, while the closer pen ensured that the wolves would not be able to see their packmates, but would be able to hear them. The researchers recorded howls produced while the three wolves were placed in the pens. Analysis of the howls was conducted by ear and audio-spectrograph. There are significant differences between the howls of different wolves. Theberge & Falls (1967) suggest that each wolf's howl is "at least potentially recognizable by other wolves". Therefore, wolves may use these howl variations to recognize and communicate with each other. These variations could help organize movements among wolves by being useful in locating isolated packmates and alerting other packs of occupied territories. The authors suggest that more studies based on analyzing the variation in howls between individual wolves are needed as the sample size in this study was very small. Further investigation is also needed to determine what information is included in the different variations of howls.

**Contribution:** This article was included in my literature review because, at the time of publication, it provided new insights into the acoustics of wolf howls. This research advanced knowledge in the field by analyzing the differences of individual wolf howls and suggested possible reasons for why these variations may exist. These results support previous findings that suggest that the activity a wolf is doing influences the tone of their howl.

Zaccaroni, M., Passilongo, D., Bucciante, A., Dessì-Fulgheri, F., Facchini, C., Gazzola, A., Maggini, I., & Apollonio, M. (2012). Group specific vocal signature in free-ranging wolf packs. *Ethology Ecology & Evolution*, 24(4), 322–331.

<https://doi.org/10.1080/03949370.2012.664569>

**Contribution:** Previous work has shown that individual wolves are distinguishable based on individual differences in the lowest note of their howl. This study aimed to determine if chorus howls differ in the same way that individual howls do and if these can be used to identify distinct packs. Zaccaroni et al. (2012) played recordings of howls to trigger a howling response from wild wolves in Tuscany, Italy from 2007-2009. The howling responses were recorded with a microphone. Spectrograms were then made for these recordings to allow the researchers to analyze the differences between the chorus howls of different packs. Twelve variables for each howl were analyzed. Variables were analyzed one at a time, as well as in groups of two or more. There were significant differences between 10 of the variables when analyzed independently. Furthermore, analyses of multiple variables simultaneously showed that each pack of wolves had a distinct chorus howl structure. Even though the individuals in a pack changed from one year to the next, chorus howls were still distinguishable between packs year to year. This suggests that a chorus howl may still be useful in recognizing different packs after an extended period of time. The authors suggest that further research is required to determine whether genetics cause these differences between chorus howls or if there is another explanation.

**Summary:** This article was included in my literature review because it provided new insights into how chorus howls differ between packs. This research advanced knowledge in the field by suggesting that chorus howls differ between packs similarly to how howl differ between individuals. This paper also provides insight into how these differences in group howls are a possible way humans can recognize different packs, as well as different packs recognize each other. This report supports previous findings that predict that the territorial nature of wolves should lead to the evolution of distinct chorus howls.

Palacios, V., Font, E., Márquez, R., & Carazo, P. (2015). Recognition of familiarity on the basis of howls: A playback experiment in a captive group of wolves. *Behaviour*, 152(5), 593-614. <https://doi.org/10.1163/1568539X-00003244>

**Summary:** Previous research has shown that the lowest frequency and pitch changes in a wolf howl can be used to recognize different wolves. This study aimed to investigate whether wolves actually use these distinct howl characteristics to identify other wolves. Palacios et al. (2015) studied a pack of seven captive wolves from November to December in Senda Viva Park (Spain). The methodology had two stages: “habituation” and “habituation-dishabituation”. In the “habituation” stage, the same recording of a howl was always played. This became the “familiar stimulus.” During the “habituation-dishabituation” stage, the “familiar stimulus” recording was played twice, then four more recordings of different howls or modified versions of the “familiar stimulus” howl were played. To change the “familiar stimulus” howls, their lowest frequency and/or pattern of pitch changes were adjusted. Researchers observed the behavioural responses, including the movements of the wolves in response to hearing the howl recordings. Wolves responded by changing their behaviour in response to howls that had their lowest note changed drastically. They did not change their behaviour in response to smaller changes to the lowest note of the howl or changes to the pattern of pitch changes. These results suggest that wolves may be capable of recognizing the differences between the howls of different wolves. The researchers proposed that wolves only behaved differently to large changes in the lowest note of the howl because wolves naturally change the lowest note of their howls within a small range. The authors suggest that further research is needed to determine how wolves use these differences between howls to distinguish between different individuals.

**Contribution:** This article was included in my literature review because it provides new insights into how wolves can recognize other wolves based on their howls. This research advances knowledge in the field by determining which part of a howl is used by wolves to recognize one another. These results support findings in other studies that found that there are significant variations between lowest note of individual wolf howls and that these variations in lowest notes are one of the best variables to tell individuals apart.

Harrington, F. H., & Mech, L. D. (1983). Wolf pack spacing: Howling as a territory-independent spacing mechanism in a territorial population. *Behavioral Ecology and Sociobiology*, 12(2), 161–168. <https://doi.org/10.1007/BF00343208>

**Summary:** Previous work has shown that wolves advertise their territory through chemical and auditory signals (scent marking and howling) to prevent running into other packs. It has been shown that wolves increase the amount of scent marks that they leave in areas where their territory converges with the territory of another pack. This study aimed to investigate whether a wolf's location in its territory also impacted its howling frequency to advertise its territory. From 1972-1974, Harrington & Mech (1983) used radio-tracking to study the movements of wolves in response to recordings of howls meant to imitate a wolf encroaching on their territory. The howl recordings were only played when the researchers were sure that the observed wolf was stationary so they could be sure that any movement was in response to their howl recordings. Researchers also noted if the wolf howled back in response to the recordings. The boundaries of the territories occupied by each wolf was determined to compare each wolf's response to the howl recordings relative to their location in their territory. Wolves did not seem to behave differently to the imitation of an intruding wolf depending on their location within their territory. If wolves responded by howling back, they typically did not move from their location. If wolves did not respond by howling back, they withdrew and moved somewhere else. These results suggest that when howling is used for inter-pack communication, it is "a location-independent avoidance mechanism". Since confrontations between unfamiliar wolves lead to conflicts, inter-pack howling may be used to enforce the territoriality of wolves and prevent accidental meetings. Some wolf packs change territories throughout the year, and the authors suggest that future work is needed to determine if howling is used for territorial reasons in these packs as well.

**Contribution:** This article was included in my literature review because it provided new insights into interactions between different packs. Although it was known that howling is used by wolf packs to advertise territories, this research advanced knowledge in the field by suggesting what types of information may be included in inter-pack howling to prevent meetings between unfamiliar wolves. These results support previous findings that howling plays an important role in wolf territorial behaviour.

Harrington, F. H., & Mech, L. D. (1979). Wolf howling and its role in territory maintenance. *Behaviour*, 68(3–4), 207–249. <https://doi.org/10.1163/156853979X00322>

**Summary:** Previous work has shown that howling can be used within a wolf pack as well as between packs to communicate. This study aimed to determine the role and importance of inter-pack howling and its purpose in wolf territorial behaviour. Harrington & Mech (1979) radio-tracked wild wolves from eight packs and 10 lone wolves in the Superior National Forest in Minnesota from May 1972 to March 1974. The researchers mimicked wolves by producing howling noises and recorded the howls of the studied wolves in response. Two or three howls were recorded from each wolf. Any movements by the wolves in response to the howling noises were also noted. Several factors seemed to influence how often wolves responded by howling back, including pack size, presence of pups, kills, breeding season, and social role. The presence of defendable resources, such as kills and young, seemed to have the largest influence on howling used for territory maintenance. When these resources were present, wolves were more likely to respond to the howling noises produced by humans. No movement was typically observed from wolves who responded by howling back. Wolves moved away from their location if they did not howl back. This suggests that howling may play a role in mediating movements between unfamiliar wolves so that they can avoid conflicts. Solitary wolves were less likely to howl back in response to the human howls relative to wolves in packs, suggesting that pack size lowers their worry that producing loud audible signals might lead to them being attacked. The authors suggest that future studies are needed to determine how far the sound of a wolf howl can travel so that it can still be used as an effective form of communication.

**Contribution:** This article is included in my literature review because it provides a good overview of the major social factors that influence howling in wolves. This article provides new insights into how reply rates increase or decrease depending on pack size, presence of pups, and social role, and advances knowledge in the field by suggesting which of these factors influence the frequency of howling replies the most. These results support findings in other studies that suggest that howling elicits different responses depending on whether the receiver is from the same or different pack than the signaller.

Ausband, D. E., Bassing, S. B., & Mitchell, M. S. (2020). Environmental and social factors influencing wolf (*Canis lupus*) howling behavior. *Ethology*, 126(9), 890–899.  
<https://doi.org/10.1111/eth.13041>

**Summary:** Previous work has found that some social influences on wolf howling include organizing group movements, alerting group members of predators nearby, and protecting the pack's territory. This study aimed to determine how the size of a wolf pack might change how wolves respond to other howls. Furthermore, this study considered how human influences of wolves, such as hunting, might influence their howling behaviour. Ausband et al. (2020) studied 4,172 areas occupied by wolves in Alberta and Idaho from 2007-2018. Researchers imitated wolf howls and produced a sequence of five howls at each location. This sequence was repeated multiple times at each location and the number of times that wolves responded by howling back was recorded. Humans participating in hunting did not seem to significantly increase or decrease how much wolves responded to the howl imitations. This suggests that hunting may not have a permanent impact on wolf howling behaviour. Furthermore, larger groups were less likely to howl back relative to smaller groups, contradicting results from other studies. Additionally, older pups (16-18 weeks old) were more likely to respond compared to younger pups (less than 16 weeks old). This suggests that howling is used by wolves to locate pups upon returning from getting food for them and to warn predators to keep away. This contrasts other studies that show that wolves generally use howling in situations such as conveying one's competitive abilities. The authors suggest that future studies are needed to determine if natural selection will favour wolves who howl less during the pup-rearing season if humans use the sounds of howling to locate where wolves raise their pups while they are hunting.

**Contribution:** This article was included in my literature review because it provides new insights into how social factors that influence wolf howling may change their behaviour depending on the time of year. The research in the article advances knowledge in the field on how the use of howling in pup-rearing season is different compared to other times in the year. This contrasts other studies that have found social factors that influence wolf howling generally throughout the year. Furthermore, this research demonstrates the differences in howl use by wolf groups of different sizes.

Mazzini, F., Townsend, S. W., Virányi, Z., & Range, F. (2013). Wolf howling is mediated by relationship quality rather than underlying emotional stress. *Current Biology*, 23(17), 1677–1680. <https://doi.org/10.1016/j.cub.2013.06.066>

**Summary:** Previous work has found that pack size influences how frequently wolves howl and that howling is a way that wolves locate isolated members of their group. This article aimed to determine whether the social rank of isolated packmates or the bond strength with isolated packmates impacts howling. Mazzini et al. (2013) determined the social rank of every individual in a captive wolf pack and determined which individuals had the strongest bonds. Nine of the wolves in the pack were subjected to both test and control conditions. In the test conditions, each of the nine individuals were removed one at a time from the pack so that their packmates did not know where they were. In the control condition, each individual was placed in an area away from the pack so they could not see each other, but their packmates were still aware of their location. For twenty minutes after the separation, the number of howls emitted from the pack was recorded and then saliva samples were collected to measure for cortisol levels. Cortisol levels and howl frequency significantly increased in response to test conditions, suggesting that not knowing the location of a packmate was stressful. Removal of high-ranked individuals also increased howling rate and cortisol levels. Removal of individuals with strong bonds to their packmates resulted in increased howling, but no change in cortisol levels. These results may suggest that howling is not always triggered by stress. Howling is a way to connect and reunite with prominent packmates. Since stress did not act as the trigger for howling when individuals with strong bonds to their packmates were separated, howling may be under control by cognition. The authors suggest that future research is needed to determine the neurobiology of howling in wolves.

**Contribution:** This article was included in my literature review because it provides new insights into when howling is used to locate isolated pack mates. The research in this article advances knowledge in the field by demonstrating that the rank and bond of the isolated individual influences the amount that their pack mates howl to try and locate them. These results support previous findings that the same things influencing audible signalling in other species such as chimpanzees.

**Watson, S. K., Townsend, S. W., & Range, F. (2018). Wolf howls encode both sender- and context-specific information. *Animal Behaviour*, 145, 59–66.**  
<https://doi.org/10.1016/j.anbehav.2018.09.005>

**Summary:** Previous work has shown that intra-group howling is used to locate isolated individuals, while inter-group howling is used in territory maintenance. This study aimed to determine whether context (territory maintenance or communicating with isolated individuals) influences the acoustic differences of howls. Watson et al. (2018) recorded all howls from captive wolves at the Wolf Science Center in Austria from June 2012 to March 2013. The observers also noted whether the howl was produced for territorial reasons or to communicate with packmates. Differences in the howl structures were compared by listening to the howls by ear, as well as through spectrogram analysis. Several variables were compared between different howls, such as the length of the howl and the average lowest note. The phenotype of the wolf was also considered to determine whether it had an influence of howl structure along with context. After analyzing 913 howls produced by nine wolves, results suggested that phenotype did not influence call structure. However, there were significant differences between howls produced during territorial calls compared to calls used to locate packmates. These results suggest that context is distinguishable by howl acoustics, as the context may increase the howl rate of an individual and influence other variables such as the volume of their call. The authors suggest that further research is needed to determine whether wolves are able to recognize these contextual differences in howl structure.

**Contribution:** This article was included in my literature review because it provides new insights into how wolf howl structure is different depending on why the wolf is howling. This research advances knowledge in the field by presenting visual representations of howl structures (spectrographs) to show these differences. The results support findings in other studies that suggest that wolves have unique howl structures due to factors such as body size. However, this study contradicts previous work that suggests that chorus howls between packs differ. This contradiction could have been caused due to a small sample size.

Harrington, F. H. (1987). Aggressive howling in wolves. *Animal Behaviour*, 35(1), 7-12.  
[https://doi.org/10.1016/S0003-3472\(87\)80204-X](https://doi.org/10.1016/S0003-3472(87)80204-X)

**Summary:** Previous research has shown that deeper vocalizations of animals can be used to convey competitive abilities to opponents. It was also known that wolves typically respond to howls while approaching the signaller during aggressive interactions. This study aimed to determine whether howling in wolves followed this trend of being deeper in pitch in hostile contexts. Harrington (1987) used data from his previous study (Harrington & Mech, 1979, see above) where recordings of howls were collected in response to humans imitating wolf howls and any movements of the wolves being studied were noted. Harrington (1987) also collected howl recordings and movement changes from wolves in response to recordings of adult and pup howls to see if the age of the signaller influenced the behaviour of the receiver. To ensure that differences between aggressive and non-aggressive howls could be detected, howls were recorded from the same wolves when they were not showing any hostility. The recordings of the howls were analyzed visually by sonograph. In every instance where wolves were howling in aggressive contexts, their howls had a significantly deeper pitch than non-hostile howls. Occasionally, the aggressive howls also had a “broken voice quality,” which was not present in non-aggressive howls. These results suggest that when a wolf moves closer to the signaller while howling, they are attempting to communicate their competitive abilities to persuade the other wolf to leave. This is important for wolves as encounters between wolves belonging to different packs often lead to injuries or death. Although larger body sizes correspond to deeper vocalizations in many species, this study only showed this trend in pups, meaning as pups got older, their voices became deeper. The author suggests that further research is needed to determine if this trend is also true for adult wolves.

**Contribution:** This article was included in my literature review because it provides new insights into how aggressive and agonistic interactions between wolves influence their howl structure. This research advances knowledge in the field by providing evidence that supports that howl pitch decreases significantly in aggressive contexts compared to howls in non-aggressive interactions. These results support findings in other studies of other species that suggest that call pitch decreases to convey an individual’s competitive abilities.