



universität
wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

“The Effect of Chorusing on the Acoustic Structure of Wolf
Howls”

verfasst von / submitted by

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angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of
Master of Science (MSc)

Wien, 2022 / Vienna, 2022

Studienkennzahl lt. Studienblatt /
degree programme code as it appears on
the student record sheet:

UA 066 878

Studienrichtung lt. Studienblatt /
degree programme as it appears on
the student record sheet:

Masterstudium Verhaltens-, Neuro- und
Kognitionsbiologie

Betreut von / Supervisor:

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Acknowledgements

First and foremost, I would like to thank my supervisors, Prof. Tecumseh Fitch, PhD for introducing me to the most fascinating world of bioacoustics, and Associate Prof. Friederike Range, PhD for welcoming me at the Wolf Science Center, a place of great camaraderie and hands-on science that will always hold a very special place in my heart.

Special thanks to Pablo Arias, PhD, whose expertise in statistics and Python programming were an integral part of this project and who was an unshakeable pillar of support throughout the analysis and beyond.

I also want to thank all the friends I've made at the WSC, from students to staff, for the treasure trove of unforgettable memories and a newfound sense of confidence that I didn't know I could develop. Jade, Lexa, Nina, Lena, Alex, Esther, Laura, Sophie, Kim, Monika, and so many others – I hope we see each other again.

Thanks to my friends at home - Stephanie, Hans-Peter, Gunnar, Christiane – for always having a kind word when I needed one.

And last - but very much not least - I want to thank my biggest supporters, my mother Sabine and father Franz, as well as my partner Akshay, whose belief in me supersedes my own and without whom I would have sunk into a hole I couldn't have escaped from alone.



Zusammenfassung

Timberwölfe (*Canis lupus*) sind hochsoziale Raubsäugetiere, deren soziale Interaktionen häufig von Vokalisationen begleitet werden. Ihr bekanntester Ruf ist das Heulen, welches vornehmlich der Gruppenkohäsion im weiteren Sinne dient. Dennoch kommt es vor, dass Individuen alleine heulen. Es ist hinreichend belegt, dass Heuler allein durch ihren akustischen Aufbau einem bestimmten Individuum zugeordnet werden können, wobei gewisse Kontexte (aggressive Interaktionen, Separation von Rudelmitgliedern) diese akustische Struktur beeinflussen können. Meine Studie beschäftigt sich mit den potentiellen Unterschieden der akustischen Struktur von solitären Heulern (begrenzt von 5 Sekunden Stille davor und danach) im Vergleich mit Geheul, das produziert wird, wenn ein Rudelmitglied zeitgleich heult (mit einer zeitlichen Überlappung von mindestens einer Sekunde). Ich habe sechs Rudel in Gefangenschaft (Wolf Science Center, Ernstbrunn, Österreich) beim Heulen während der Morgen- und Abenddämmerung und während ein Rudelmitglied aus der Gruppe genommen wurde beim Heulen aufgenommen. Die Analyse von 100 solitären Heulern und 120 Heulern mit Rudelmitglied hat ergeben, dass letztere signifikant variabler sind als solitäres Geheul und eine größere Bandbreite an Frequenzen umfassen. Grund für diese Unterschiede könnte sein, dass der individuelle Erkennungswert bei solitärem Heulen im Vordergrund steht, während beim gemeinsamen Heulen eher die Rudelpräsentation gegenüber anderen Rudeln wichtig ist (vergleichbar mit der Beau-Geste-Hypothese bei Singvögeln). Zukünftig sollten jedoch zusätzliche Faktoren wie begleitende Verhaltensweisen und Reihenfolge von heulenden Individuen hinzugezogen werden, um robustere Schlüsse über Motivation und deren Einfluss auf bestimmte akustische Muster ziehen zu können.

Abstract

Timber wolves (*Canis lupus*) are a species of highly social predatory mammals whose social interactions are often accompanied by a range of vocalisations, most famously the howl. Though howls mainly serve group cohesion, solitary howling does occur as well. It is well documented that individuals can be identified by the acoustic features of their howls alone, although aggressive or separation contexts are known to influence their structure. In this study I aimed to investigate a possible difference between the acoustic features of solo howls (defined as howls bordered by five seconds of silence) and chorus howls (defined as howls that temporally overlap a pack member's howl for at least one second). I recorded a population of six captive wolf packs housed at the Wolf Science Center in Ernstbrunn, Austria, during dawn and dusk, and opportunistically when an individual was separated from its pack. Analysing the fundamental frequency contours of 100 solo howls and 120 chorus howls, I found that chorus howls were significantly more varied and encompassed a greater range of frequencies. I concluded that individual recognition is more important for solo howls, whereas chorusing serves as an inter-pack communication and might represent something akin to the Beau Geste effect in songbirds. However, a more granular approach is advisable for future studies to draw more robust conclusions about the influence of contextual circumstances on the acoustic structure of wolf howls.

Introduction

One of the defining features of humans is, without a doubt, our ability to encode vast amounts of information through the use of speech. We are able to rapidly (re-)shape our vocal tract to achieve the great variety of sounds we know as the acoustic building blocks of our communication (Fitch, 2000). It is a topic that is as complex as it is fascinating; there are cognitive, genetic, neurological, social, cultural, and ontogenetic factors that influence how, when, and why we produce speech. It begs the question: What circumstances might have facilitated the emergence of this highly flexible and practically open-ended communication? As fossil evidence has proven largely unhelpful, focus has shifted towards comparative biology as the main tool to investigate which social challenges shape the production, usage and perception of a given species' vocal repertoire, since the acoustics, physiology and neural control of sound production are shared between humans and non-human animals (Fitch, 2000).

Vocal Flexibility and Chorusing

There are two main parts to what makes a vocalisation flexible: its acoustic features (e.g., duration, range and variation of frequencies) and its use (e.g., audience effects, social context and/or function). Interactions with conspecifics are inherently unpredictable and risky; a caller can reduce this uncertainty by assessing their variable social environment and tuning their utterances accordingly (Seyfarth and Cheney, 2018). Past studies have shown that abilities such as the modification of vocal tract morphology and vocal imitation are not restricted to a certain taxon, but instead can be found in a variety of species (Fitch, 2000). One example is the African grey parrot Alex, whose capability of asking and answering questions using rudimentary English sentences made him famous beyond the boundaries of academic spaces (Pepperberg, 1987). Another is the well-known signature whistle of bottlenose dolphins, which are passed down from mother to male calf, while female offspring develop their own signature whistle (Sayigh et al., 1990). Especially interesting for our study is the finding that male chimpanzee dyads acoustically converge their long-distance call, the so-called "pant-hoot", with each other when chorusing together (Mitani and Gros-Louis, 1998). Mitani and Gros-Louis (1998) suggest in their paper that this form of vocal accommodation might be present in a variety of other taxa, where the strengthening of social bonds is beneficial to the individual. Wolves' daily lives are dominated by constant interactions with conspecifics, strong social bonds between pack members, and they are famously known for their long-distance call, the howl. This makes Timber wolves (*Canis lupus*) an interesting candidate for the examination of their vocal responsiveness to changing social contexts.

Timber Wolves (*Canis lupus*)

Ecology

Wolves (*Canis lupus*) are large predatory mammals who thrive in a multitude of habitats across the northern hemisphere, from the tundra and frigid mountains to deserts and even swamps. Their body size follows Bergmann's rule, which dictates that individuals in hotter climates (e.g. Israeli wolves, measured at under 15kg) are smaller than their arctic cousins (measured at up to 80kg) (Mech and Boitani, 2003). While generally classified as cooperatively hunting carnivores, they do not shy away from scavenging carcasses or seasonal fruits and berries (Mech and Boitani, 2003). If that alone does not already speak for their variability and adaptability, one can look at the various levels of their complex social life, from the interactions of dispersing lone wolves looking for a new pack with a suitable mating partner, to intra- and inter-pack social dynamics.

The core of the lupine social life is the pack. A pack is formed when sexually mature males and females, who dispersed from their original packs, come together to form a breeding pair. A litter contains up to six pups, who do not reach sexual maturity until 22 months of age (Mech, 2012a). Since litters occur annually under suitable conditions, the older (not yet mature) siblings often partake in the care of the younger through socialisation, guarding and food sharing (Mech, 2012b), making the wolf a species of cooperative breeders. The offspring typically disperse between five to 36 months of age and form their own packs (Boitani and Mech, 2003). This information serves as a useful rule of thumb, though observations of wild wolf packs paint a much more complicated picture. Numbers can reach up to 41 individuals per pack (Mech and Boitani, 2003), which cannot be explained by yearlings staying with their parents alone. There are sightings of wolves who travel freely between packs and care for pups in both packs during a single denning season (Boitani and Mech, 2003). Additionally, there are accounts of multiple breeding females in one pack, and some wolves have even been observed to be friendly towards one individual of a different pack, but not another. This suggests that social bonds, without which no pack cohesion or cooperative hunting and breeding would be possible in the first place, play a larger role in pack formation than strictly biological or environmental conditions (Mech, 2012a). In conclusion, this highly social species is an interesting model regarding the possible interplay between social bonds, cooperative breeding, and vocal communication.

Wolves communicate constantly using scent markings, body posturing and facial expressions, as well as vocalisations, the latter of which accompany many of the wolves' social behaviours (Harrington and Asa, 2003; Mech, 2012c). Not unlike our own offspring, wolf pups are very vocal from birth, albeit within a repertoire that is suitable to their needs as highly dependent and mostly immobile den-residents. Their cries rarely exceed three seconds in length and are naturally very high-pitched, thanks to their small vocal folds (Harrington and Asa, 2003; Schassburger, 1979). At about three weeks of age, this repertoire of squeals, screams, yelps and yawns gradually gives way to the full range of adult vocalisations, which Schassburger (1979) split into the following general categories: harmonic or noisy, short-ranged or long-ranged. He found harmonic sounds to be correlated with friendly or submissive behaviour or interactions, and noisy ones with aggressive or dominance contexts. Schassburger labelled short-ranged harmonic sounds as whimpers, whines, or yelps, and noisy ones as woofs, growls, barks, and snarls. These vocalisations can also occur mixed (e.g., growl-bark), which he interpreted as a functional summation or as a grading of intensity. These man-made classifications should not be taken as rigid or universally accepted though; other researchers draw the lines differently, mostly in regard to how broad or narrow a useful category should be (see also Joslin, 1966 or Theberge and Falls, 1967 for different "splitter" or "lumper" approaches).

Acoustic signals have several advantages as a means of communication: they can be modulated quickly and extensively, they travel fast and far, do not need line of sight, or the audience's initial attention. This plays heavily into the wolves' famous long-range call, the howl. As howls travel long distances, they are subject to environmental distortions and information loss (especially in higher frequencies). To counteract those losses, long-distance calls should be lower and harmonically purer, features we can observe in howls when compared to other wolf vocalisations (Harrington and Asa, 2003). Generally, howls can last anywhere from under a second to fourteen seconds, with the mean duration lying between three and seven seconds (Harrington and Mech, 1978; Schassburger, 1979; Theberge and Falls, 1967). Their fundamental frequency range lies between 150Hz and 1000Hz, averaging at 300-670Hz (Harrington and Asa, 2003). Most of the energy resides within the fundamental frequency and the first two harmonics (Harrington and Asa, 2003). Modulation can be highly complex or "flat", and the pitch contour can be discontinuous ("breaking howls") (Harrington and Asa, 2003). They can travel over 10km in forested habitats (Harrington and Mech, 1978) and up to 16km in the tundra (Henshaw and Stephenson, 1974). Daily activity peaks in the mornings and evenings, with the breeding season (around February) being the busiest time of the year overall (Klinghammer and Laidlaw, 1979; Schassburger, 1979).

Rival packs will sometimes answer to a calling group (Harrington and Asa, 2003; Harrington and Mech, 1979), and confrontations are often avoided by creating distance between the two. This depends, at least partially, on whether or not there is a resource to guard (dens, food sources) (Harrington and Asa, 2003; Joslin, 1966; Theberge and Falls, 1967). Harrington (1989) hypothesizes that a sort of Beau Geste effect factors into inter-pack communication, whereby a pack can suggest a larger number of members than there actually are by exaggerating their howls. That said, howling is often directed at pack members. Evidence gathered not only through playback experiments (Palacios et al., 2015), but also statistical analysis found acoustic parameters (e.g., mean f_0 , maximum f_0 , amplitude, variation, etc.) to be consistent within individuals to such a degree that identification of the caller by these values alone was possible (Root-Gutteridge et al., 2014; Sadhukhan et al., 2021; Watson et al., 2018). This provides an obvious advantage for a group of conspecifics that interacts so frequently and intimately with each other. Some howls, though, occur for no outwardly discernible reason. These “spontaneous” howls are often cause for pack members to join in a chorus, are accompanied by affiliative social actions (like nuzzling), and might be interpreted as a tool to strengthen pack relations (Harrington and Mech, 1978). Though, howling would not need to be a long-distance call if all it had to do was facilitate socio-positive behaviour. A significant portion of howls occurs when pack members are separated (Harrington and Asa, 2003; Harrington and Mech, 1978; Theberge and Falls, 1967). Harrington and Mech (1978b) refer to it as an “assembly” call, used to pinpoint and approach dispersed mates, a behaviour that has been widely observed both in the wild and in captivity (Tooze et al., 1990). Contextual plasticity of acoustic howl structures was found during such pack member separation events (Watson et al., 2018). Relationship quality is a stronger predictive factor than general separation stress for the occurrence of “assembly calls” (Mazzini et al., 2013), lending further strength to the idea that relationships are of major importance for group cohesion in wolves. Aggressive interactions are another case where acoustic howl plasticity has been observed (Harrington, 1987).

Evidence for contextual acoustic plasticity of howls together with the strong social relationships seen in packs makes comparing solitary howling and chorus howling an interesting addition to our understanding of vocal flexibility in wolves.

Aims and Predictions

This study aims to shed light on a possible difference in the features of the fundamental frequency of a wolf's howl, depending on whether the animal is calling alone or with a conspecific (in this case, a pack member).

Despite howling being individualistic enough to identify a caller (Palacios et al., 2007; Root-Gutteridge et al., 2014; Sadhukhan et al., 2021; Watson et al., 2018), these vocalisations did differ significantly between spontaneous and elicited contexts (Watson et al., 2018), indicating that underlying motivation could influence the structure of a howl. Assuming solo howls serve a different function to chorus howls, we expect the values of various fundamental frequency parameters to differ significantly between solo howls and howls emitted concurrently with a pack member.

Methods

Subjects

The subjects of this study are 17 Timber wolves (*Canis lupus*), who were housed at the Wolf Science Center (hereafter referred to as the "WSC"), Dörfles 48, 2115 Ernstbrunn, Austria (Table 1, Page 10). They formed 6 packs, ranging from 2 to 4 pack members, of which one contained no female. Adult subjects were born between 2008 and 2012. All juveniles (Maikan, Etu, Ela, Tekoa, Taima) were born in 2016. Four packs contained one pair of siblings each. All wolves were captive born and sourced either from North America or Russia.

Table 1. Overview of the subject population.

Pack ID	Name	Sex	Date of Birth	Siblings	Origin
1	Amarok	m	04/04/2012	Tala	Minnesota Wildlife Connection
	Kenai	m	01/04/2010		Park Safari, Canada
2	Geronimo	m	02/05/2009	Yukon	Triple D Farm
	Yukon	f	02/05/2009	Geronimo	Triple D Farm
	Wamblee	m	22/04/2012		Haliburton Forest, Canada
3	Kaspar	m	05/05/2008		Tierpark Herberstein
	Aragorn	m	05/05/2008	Shima	Tierpark Herberstein
	Shima	f	05/05/2008	Aragorn	Tierpark Herberstein
4	Maikan	m	04/05/2016	Taima/Tekoa	Russia
	Ela	f	04/05/2016	Etu	Canada
	Etu	m	04/05/2016	Ela	Canada
5	Nanuk	m	28/04/2009		Triple D Farm
	Una	f	07/04/2012	Chitto	Minnesota Wildlife Connection
6	Tala	f	04/04/2012	Amarok	Minnesota Wildlife Connection
	Chitto	m	07/04/2012	Una	Minnesota Wildlife Connection
	Taima	f	04/05/2016	Maikan/Tekoa	Russia
	Tekoa	m	04/05/2016	Maikan/Taima	Russia

The wolves lived in six outdoor enclosures (1000-8000m²) bounded by mesh wire and an electric fence according to local regulations (Figure 1, Page 11). The enclosures contained various amounts of shrubbery, logs, and trees, at least one wooden, unheated shelter with straw, and a drinker. Packs do not have designated home enclosures and rotate through them as needed for tests or touristic events. All packs are equally familiar with all enclosures. Enclosures are cleaned of animal waste and enriched with hidden food items once a week. All wolves participate in scientific tests, obedience and leash training, or touristic events (like trainer guided walks with visitors) at least once a week.

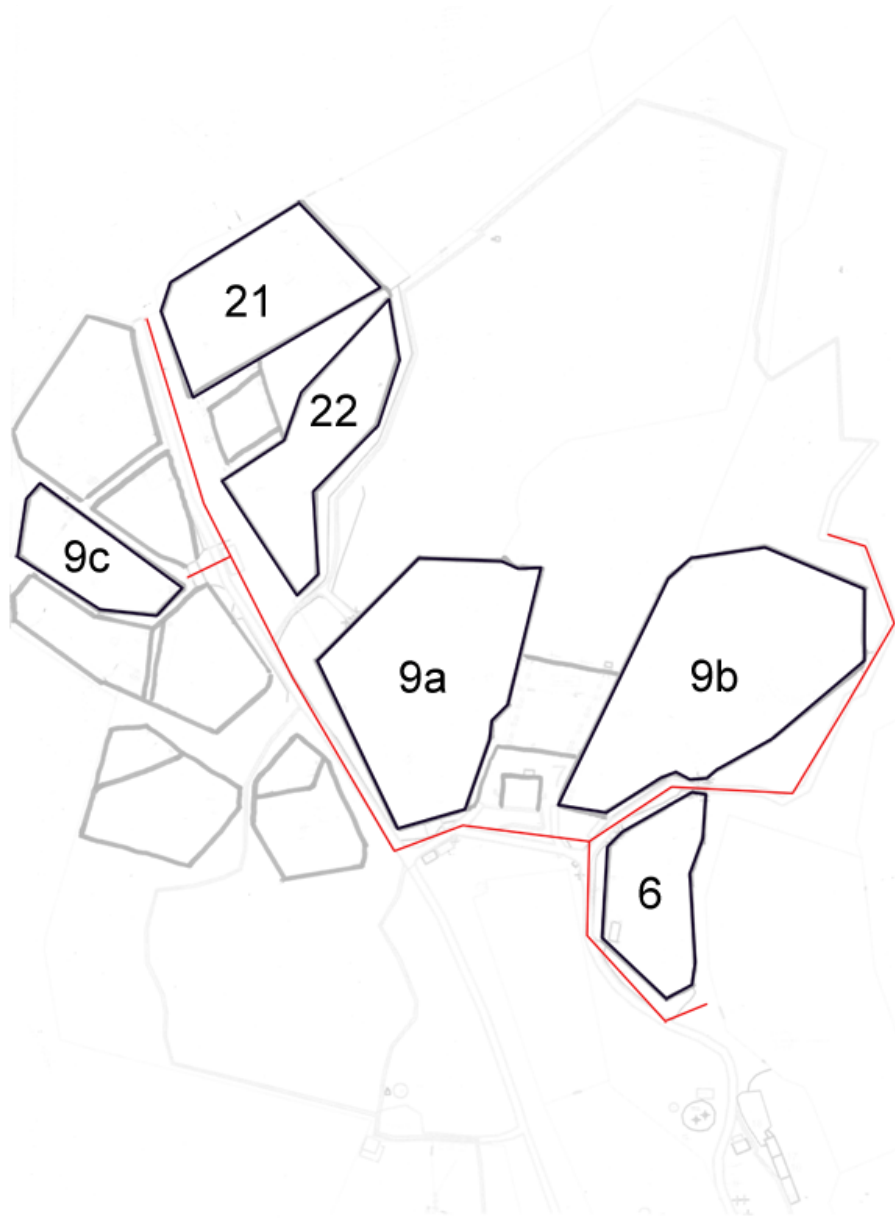


Figure 1: Layout of the enclosures in the Wildpark Ernstbrunn. Numbered enclosures house wolves, unnumbered enclosures house dogs. The red line marks accessible paths from which I recorded the animals.

Pups are separated from their mothers within 10 days of birth and are then hand raised in peer groups by multiple trainers. The pups are isolated from adult wolves for the first 5 months of their lives. They switch from being bottle fed to being fed solid foods at around three to four weeks of age. During this time, pups are kept in a special “puppy house” attached to a 1000m² outdoor enclosure, which they have unrestricted access to. Afterwards, they either form their own packs (first generation, 2008) or slowly get introduced into existing packs (later generations). To avoid uncontrolled breeding, males are vasectomised before they reach sexual maturity. Otherwise, the animals’ reproductive systems are left intact to avoid disturbing their hormonal balance which could otherwise have an undue influence on their natural behaviour. They are fed two or three times a week (depending on body condition and season), usually whole chicken or rabbits or pieces of deer, goat, or sheep.



Figure 2: Chitto stretching on a shelter in enclosure 9b.



Figure 3: A student rewarding Tala with a piece of sausage for waiting in the shifting tunnel.



Figure 4: Aragorn (foreground) howling with Shima (standing further back to the right).



Figure 5: Maikan patrolling along the frosted fence.

Data Collection

I recorded vocalisations from January to July 2017, primarily during 1-hour sessions in the mornings (6am to 8am), in the evenings (5pm to 8pm), and opportunistically during the above-described separation events at least 5 days a week. This served to avoid disturbances and background noise as much as possible (e.g., park visitors or tests), but also coincided with the times trainers have reported the animals' highest propensity to howl. Each session focussed on one pack only.

I used a directional microphone (RØDE® NTG2 or t.bone EM9900, incl. wind shield) plugged into a handheld solid-state recorder (Roland R-26; 96.0 kHz sampling rate, WAV 24-bit format) for recording. Additionally, a camera (Elephone EleCam Explorer Elite 4K Action Camera) was mounted onto the microphone handle using a bike mount to record identifying video material during sessions whenever possible (Figure 6, below). Identities were also recorded verbally within the same recording and/or manually in a notebook. The recorder was kept in pre-recording mode (thus saving the most recent 2 seconds of acoustic input) until one or more wolves started howling and returned to said mode after each howl bout was over (at least 5 seconds of silence from the focal pack). I conducted all sessions from outside the enclosure, positioning the microphone as close as possible to the animals' current position without needlessly distracting them. After each session, I documented information regarding the identity of the recorded individual/pack, whether one or more pack members were separated and why, the exact time of each recording session, the current enclosure of the observed pack, the weather condition, and any other miscellaneous disturbances in a spreadsheet. I then transferred the recorded WAV files to a PC (MS Windows 10 Pro, build 10.0.19041, x64-bit version) for further processing.



Figure 6: Picture of both microphones, the recorder, and the repurposed bicycle camera mount.

In those six months, I conducted 169 sessions total, of which 111 sessions yielded raw vocalisation data (Table 2, below). Whenever a focal pack was not chosen for counterbalancing session numbers (i.e., keeping the number of sessions recorded per pack even), it was due to outside factors like excessive background noise, weather conditions, or to avoid disturbing other scientific tests that were being conducted in parallel. As our raw data shows, howling activity is not equal across individuals and dyads. Amarok and Kenai, for example, had a high propensity to howl alone as well as together, while many of the pups (Ela, Etu, Taima) were considerably quieter (Table 3 and Table 4, below). However, not all low numbers are caused by low activity; Kaspar, for example, has a low number of solo howls because of Aragorn's tendency to join him in howling. Another factor is that due to technical limitations, we cannot consider any chorus bouts that contain more than two howling individuals. This automatically discards chorus howls by individuals that sometimes join in larger choruses but will not readily howl with certain pack members alone (e.g., Taima).

Table 2: Overview of the number of sessions conducted per pack.

Pack ID:	1	2	3	4	5	6	SUM
Sessions total	24	16	21	32	46	30	169
Sessions with howls	20	11	15	21	28	16	111

Table 3: Overview of raw solo howls per individual in descending order.

SOLO HOWLS								
MAI	KEN	AMA	TAL	SHI	UNA	YUK	GER	NAN
101	98	76	68	61	56	45	44	29
ARA	CHI	TEK	WAM	KAS	ELA	ETU	TAI	
26	17	17	14	6	5	3	3	

Table 4: Overview of raw chorus howls per dyad in descending order.

CHORUS HOWLS				
AMA/KEN	ARA/KAS	GER/YUK	KAS/SHI	GER/WAM
100	51	51	48	40
CHI/TAL	NAN/UNA	TAL/TEK	ELA/MAI	ETU/MAI
38	24	19	18	18
TAI/TEK	WAM/YUK	ARA/SHI	CHI/TEK	ELA/ETU
12	9	4	4	3
TAI/TAL	CHI/TAI			
3	1			

Data Pre-processing

To turn the raw recordings into analysable data, I opened each WAV-file in Audacity (2.1.2) and visually as well as acoustically scanned it for both solo and chorus howls. Any howl of an individual that was at least two seconds long and bordered by at least 5 seconds of silence from pack members was considered a solo howl (Figure 7, below). Any howls of two pack members that overlapped temporally for at least one second were considered chorus howls (Figure 8, Page 16). This includes sequences where one individual howled multiple times during one long, continuous howl of a chorus partner.

Once a viable howl and its corresponding animal(s) were identified, I cropped the WAV-file according to the length of the howl (or howl bout) and saved it as a separate WAV-file. The date and time of the session, type of howl, identity of the howling individual(s) and the exact position of the howl in the raw data file were recorded in a spreadsheet for each of these newly created files.

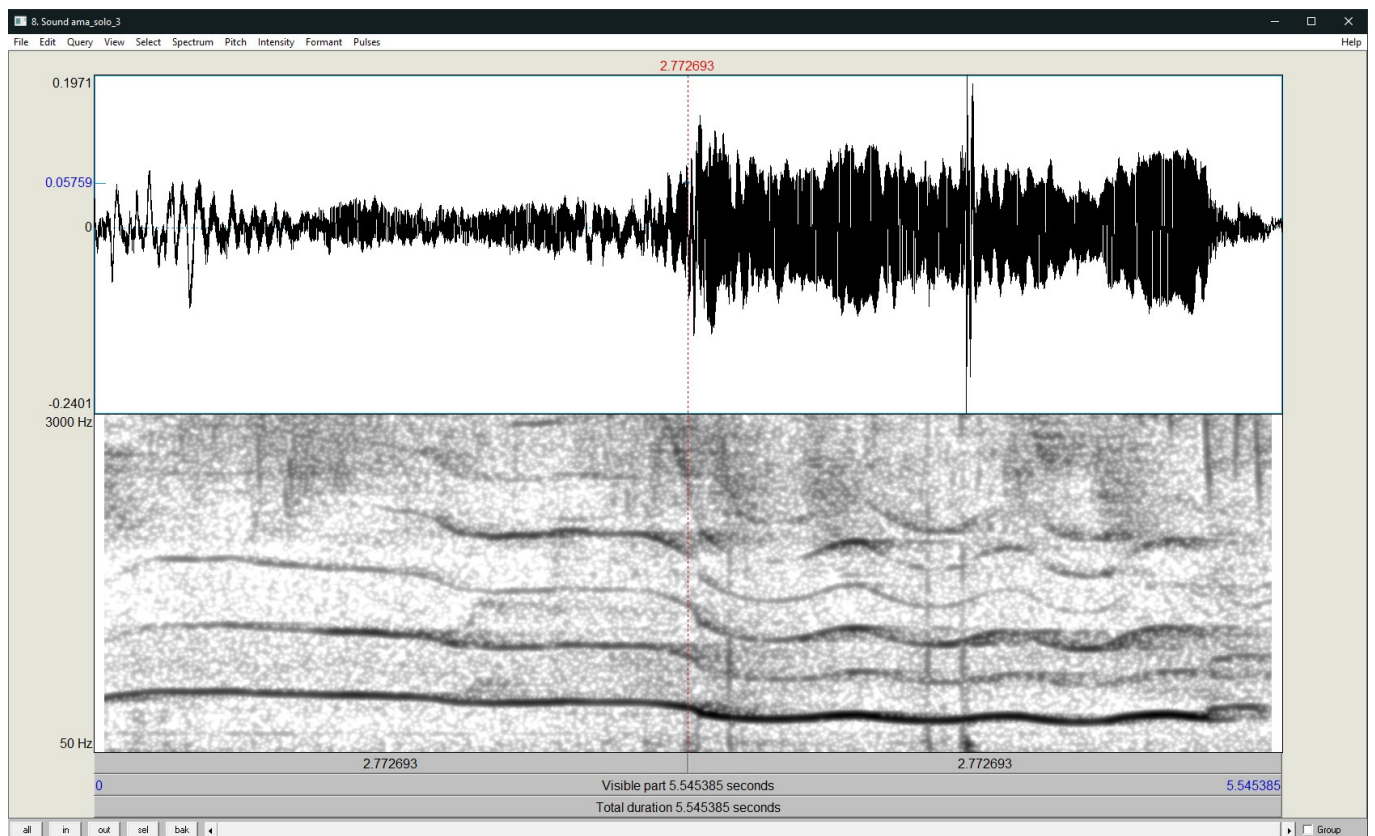


Figure 7: An exemplary PRAAT spectrogram of a solo howl.

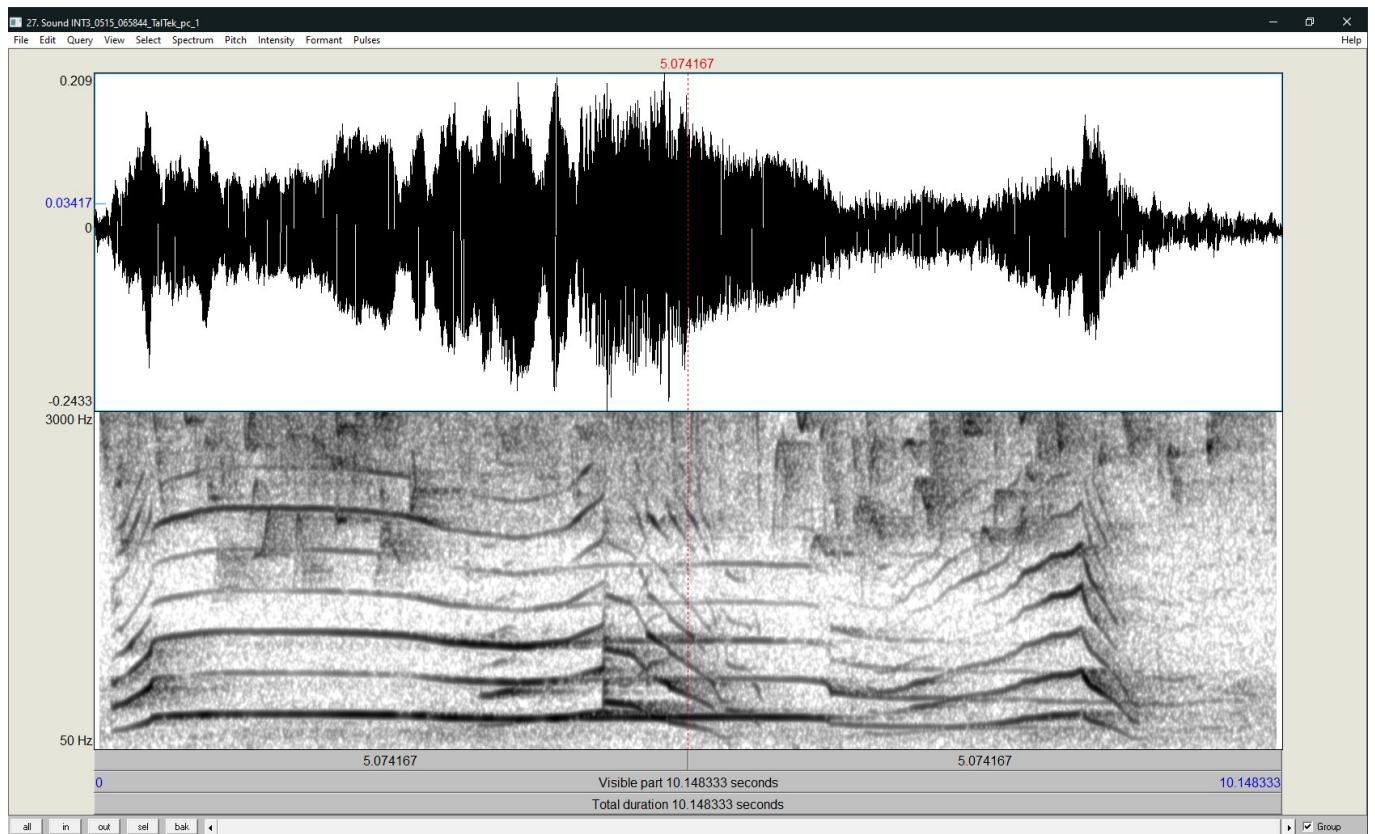


Figure 8: PRAAT spectrogram of a chorus howl of Tala and Tekoa, whose fundamental frequencies temporally overlap. Tala's shorter, peaking howls both temporally overlap with Tekoa's longer, continuous howl.

Howl tracks whose spectrograms were too visually noisy for the fundamental frequency to be tracked accurately were discarded; this included any chorus bouts with more than two individuals (see Figure 9, below, for an example).

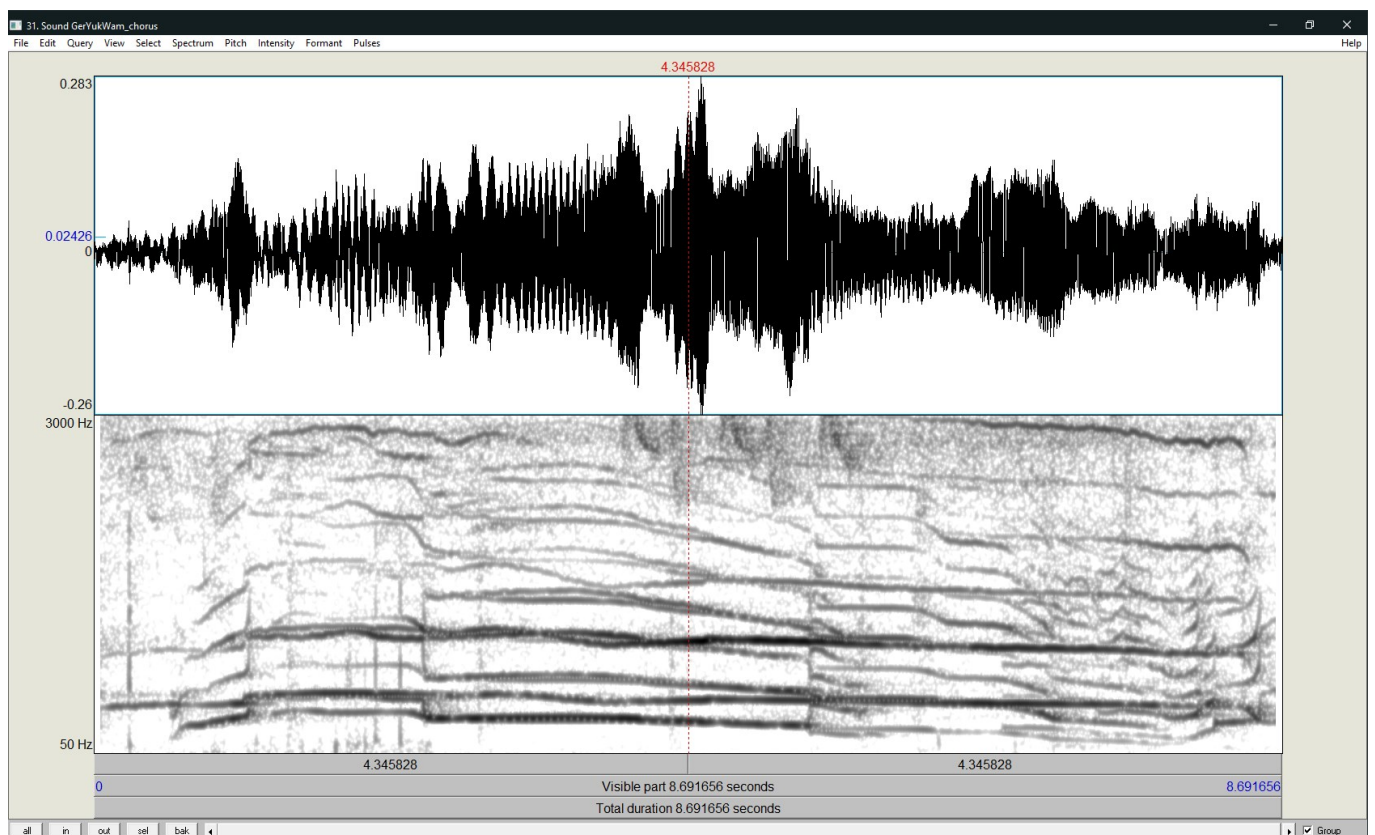


Figure 9: PRAAT spectrogram of three individuals howling together (Geronimo, Yukon, Wamlee). We were unable to trace each individual confidently and accurately due to how close together the fundamental frequencies are.

To strike a balance between including as many individuals and dyads as possible in our analysis and including a representative number of howl contours per individual, we decided to pick 10 solo howls per individual and 10 chorus howls per dyad where possible, using a random file picker in Python. The randomizer was used in each session folder separately, to ensure that it does not pick files from only a small number of sessions by chance, which would introduce undue bias. This left us with howls of 10 individual wolves (Amarok, Kenai, Geronimo, Yukon, Wamblee, Chitto, Tala, Tekoa, Nanuk, Una) and 6 dyads (Amarok/Kenai, Geronimo/Yukon, Geronimo/Wamblee, Chitto/Tala, Tala/Tekoa, Nanuk/Una), resulting in a database of 100 solo contours and 120 chorus contours.

To ensure accurate tracking of f_0 frequencies, I edited the chorus files to isolate each individual's fundamental frequency contour in a separate WAV-file. Using Audiosculpt (3.4.6), I opened a chorus WAV-file and calculated the spectrogram (samples = 4096, adaptive oversampling = 8x, oversampling = 8x, window type = Hanning). I identified the howl contours of both individuals by ear and eye, not only within Audiosculpt, but also by cross-checking the same file's spectrogram in PRAAT (6.1.08), as well as with the help of my session information spreadsheet. Figure 8 on Page 16 and Figure 10 below illustrate what the same howls look in PRAAT and in Audiosculpt.

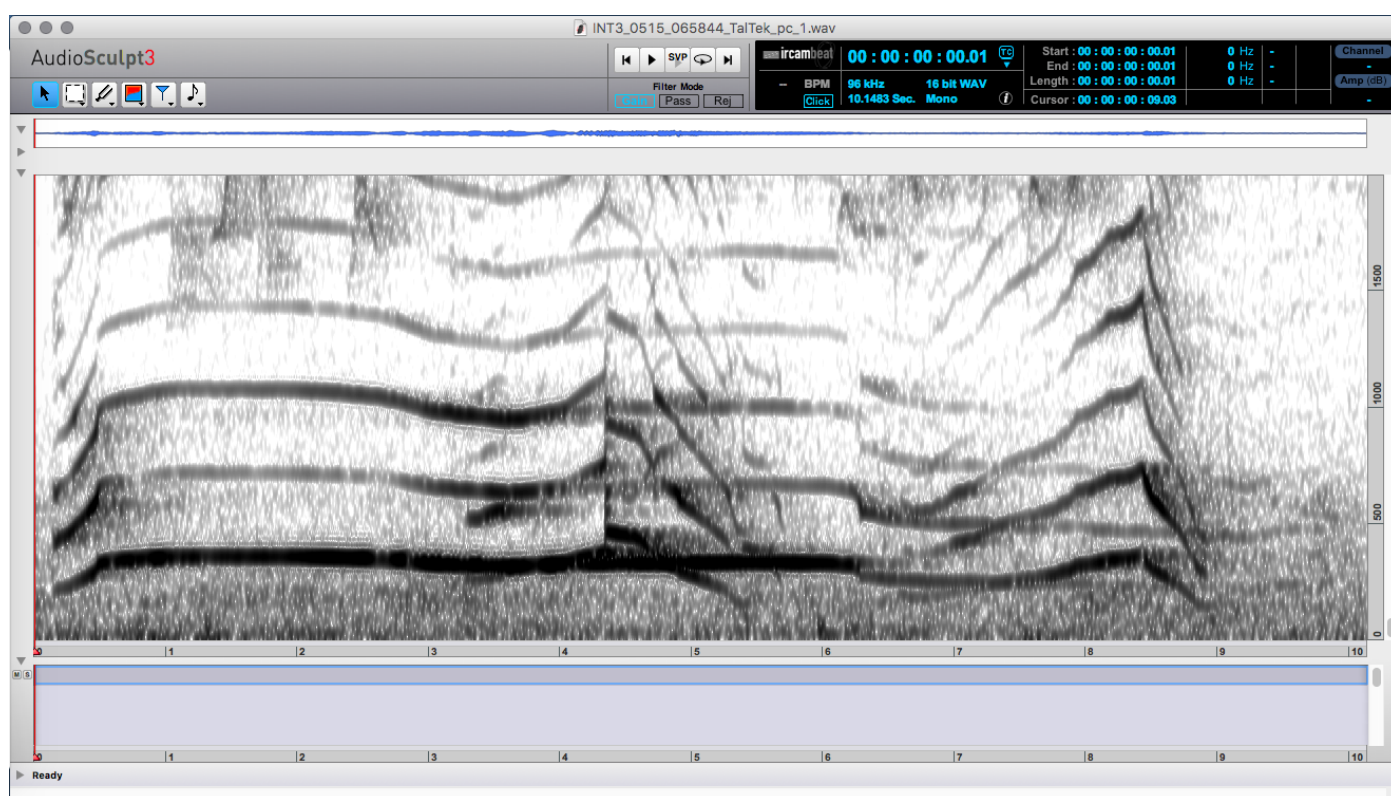


Figure 10: The same chorus howl of Tala and Tekoa from Figure 9, but in Audiosculpt. The overlap of the howls can be seen more clearly in the partials above.

By drawing rectangles using the masking tool in Audiosculpt, I masked every part of the fundamental frequency of the non-focal individual. I then selected all the rectangles by dragging the cursor across the whole spectrogram. Double clicking on any rectangle opened an editing dialogue window where I set the decibels of all selected masked areas to -80dB (Figure 11, Page 18).

Processing these treatments produced a new WAV-file with the masked fundamental effectively silenced, leaving only the fundamental frequency of the focal individual (Figure 12, below). After comparing the newly created file acoustically to the original (to ensure the vocalisation was isolated as cleanly and wholly as possible), I saved it as a separate WAV-file. I then repeated the same procedure using the original file for the other individual in the dyad.

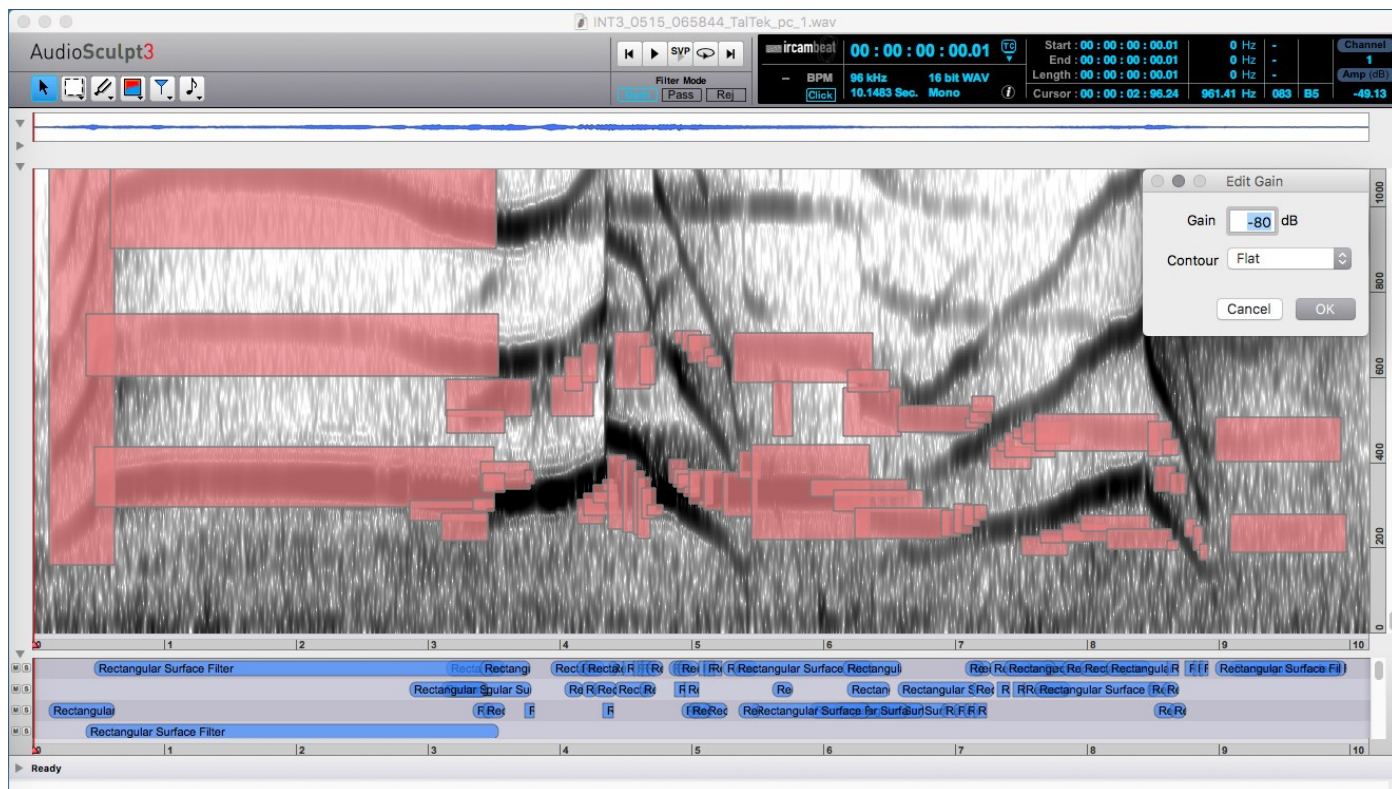


Figure 11: The fundamental and the parts of the partials of one individual (Tekoa) have been masked with the masking tool, and the gain has been set to -80dB to silence that individual, leaving only the second individual audible (Tala).

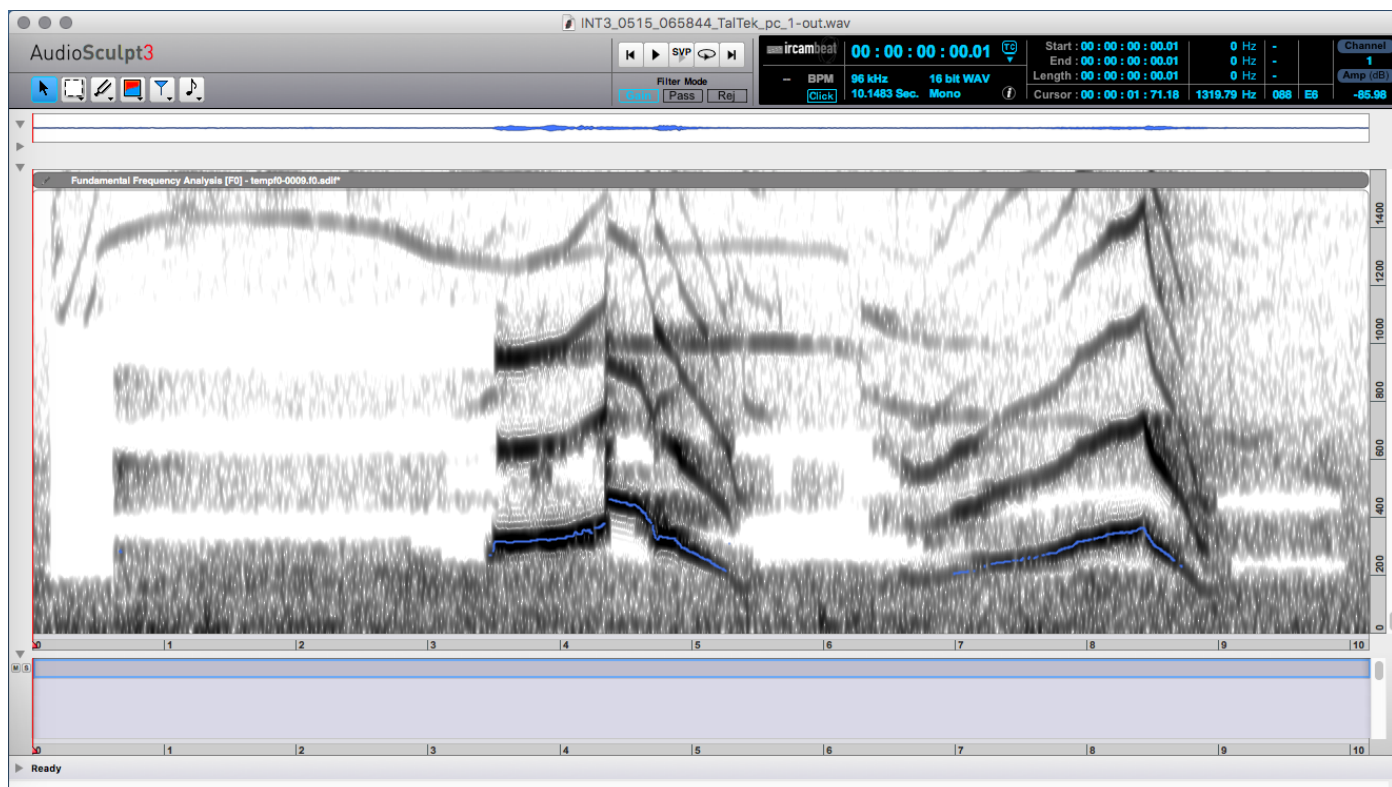


Figure 12: A look at the newly generated WAV-file. Gaps and inaccuracies in the automatically generated fundamental frequency contour arise from the noise and interfering parts that cannot be perfectly masked.

To extract f_0 -related values from both solo howls and chorus howls, I tracked the fundamental frequency in Audiosculpt3. Wherever the automatically calculated contour was visibly incorrect (e.g., due to bouts of noise), I used the pencil tool to manually trace any aberrant parts and gaps. I manually set silences to around 20-30dB to prevent information loss in the time-series later in the analysis (Figure 13, below). I then saved the frequencies and time-series values of the corrected contours as tab-separated values in TXT-files. No amplitudes were considered for this study since the background noise and the changing proximity to the recorded animals varied highly throughout the sessions, sometimes while a howl was being recorded.

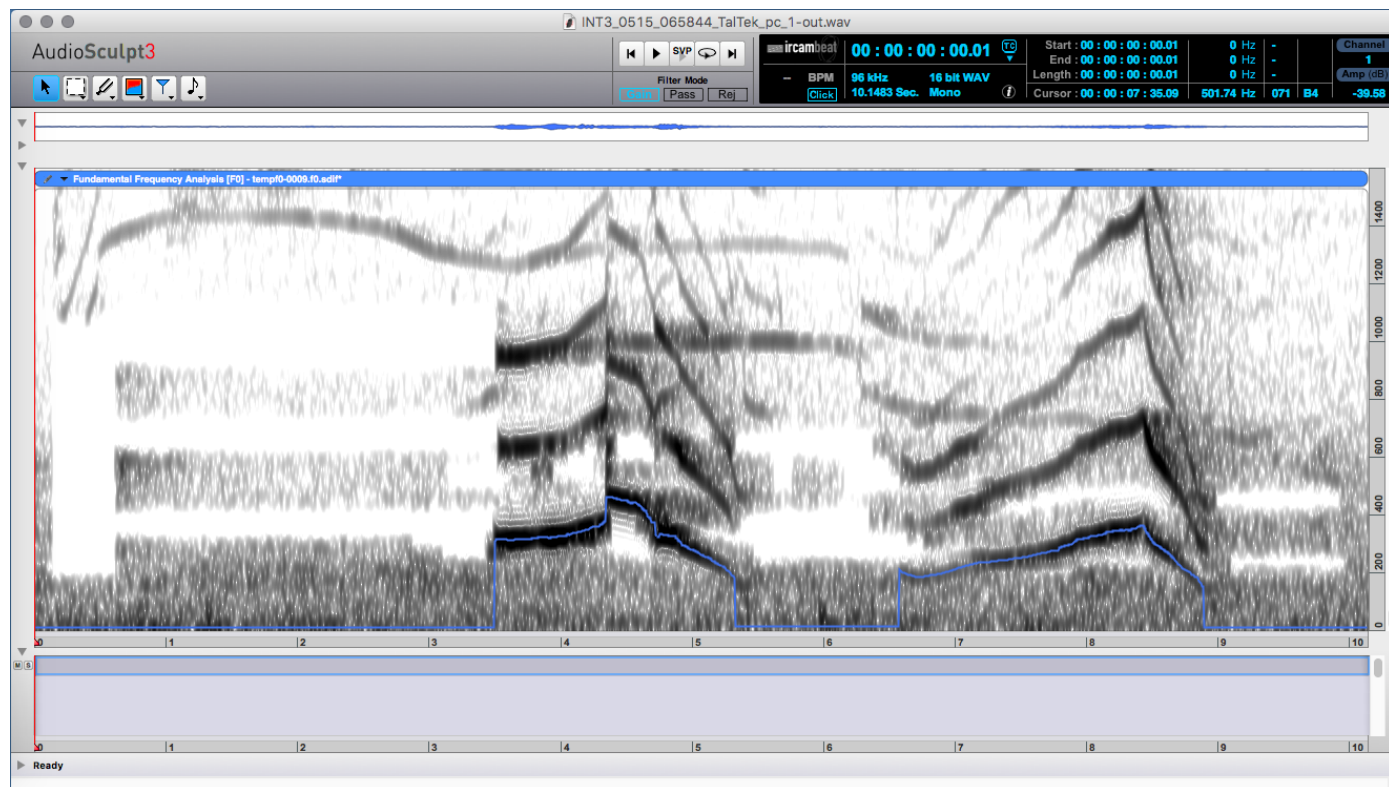


Figure 13: Manually corrected fundamental contour, using the pencil tool. Silences are manually set to approximately 30dB so they can be safely discarded in the analysis while preserving all time step values.

Data Analysis

We used bespoke Python (v3.8.4) code to:

1. Compile the database of pitch contours in a tidy data frame
2. Create figures comparing solo howl and chorus howl contours of each individual with each other and
3. Calculate descriptive statistics of the fundamental frequencies based on the values identified in the paper of Sadhukhan et al. (2021).

We considered the eight measures listed in Table 5 below.

Table 5: List of analysed variables.

Variable Name	Definition of the Variable
f ₀ _mean	The mean frequency value of the fundamental frequency contour (f ₀) over the duration of the howl
f ₀ _StDv	The standard deviation of the frequency values of the fundamental frequency contour (f ₀)
freq_range	The range of the frequency values of the fundamental frequency (f ₀), defined as Max f ₀ - Min f ₀
f ₀ _length	Length of the fundamental frequency contour (f ₀), defined as $t_{(end)} - t_{(start)}$
f ₀ _min	The lowest frequency value of the fundamental frequency contour (f ₀)
f ₀ _max	The highest frequency value of the fundamental frequency contour (f ₀)
co_var	Coefficient of frequency variation, defined as $f_0 = \sum f_{(t)} - f_{(t+1)} / (n - 1) \times 100 / \text{Mean } f_0$
co_mod	Coefficient of frequency modulation, defined as $f_0 = (SD / \text{mean}) \times 100$

For each vocalisation in the corpus, we computed each of the measures presented in Table 5. Then, we averaged these measures by individual and condition (solo vs chorus). This resulted in two measures per individual (one for solo and one for chorus vocalisations) for each acoustic descriptor in Table 5. Then, for each measure, we compared the distributions of solo vs chorus howls with paired t-tests.

As a control condition, we used bespoke code to remove silences in the contours and treat the resulting fragments as separate howls in the database. This is necessary, because one individual might produce one long howl, while another produces multiple short howls at the same time. The short howls need to be considered as separate contours (what we decided to call sub-vocalisations). The control corpus was then treated as described above.

We excluded frequencies above 1000Hz in general from the statistical analysis to remove a certain “whistling” sound one individual (Yukon) produces during some of her breaking howls.

Results

Time Series Comparisons

Our first approach was to use the `relplot` function of Seaborn in Python and plot all time-series of the solo howls and the chorus howls per individual in two separate graphs side by side, to compare them visually without any statistical analysis (Figure 14, Page 23). Each colour represents one howl. To avoid confusion, breaks in the contours are bridged with a straight line. Graphs for Yukon include the “whistling” part of her breaking howls since it is still audible and makes her recognisable. These high frequencies, which can sometimes overlap with the fundamental and do not seem to stem from her vocal folds, were discarded in the statistical analysis.

We found that while solo howls seem to be shorter and more clustered, chorus howls appeared to be longer. Individuals appeared to have broader frequency ranges during chorus howls than during solo howls. This served as the basis of our statistical analysis, which compared the eight different features of the fundamental frequency between solo and chorus.

F₀ Comparisons between Solo and Chorus Conditions

We generated bar plots for each of the eight variables across all solo and all chorus howls of the database using the `catplot` function of Seaborn in Python (Figure 15, Page 24) and compared the distributions with paired t-tests using Pingouin. See Table 6 on Page 22 for a summary of all results.

Solo howls were significantly longer (`voc_length`) than chorus howls in the test ($t(\text{voc_length}) = 3.2147$, $p = 0.0106$) condition, but the effect was lost in the control condition when we controlled for pauses in vocalisations ($t(\text{voc_length}) = 2.0688$, $p = 0.0685$).

Solo howls had a higher mean frequency (`f0_mean`) than chorus howls in both the test and the control condition, but the difference was not significant (test: $t(f_0_mean) = -1.3349$, $p = 0.2147$; control: $t(f_0_mean) = -1.3349$, $p = 0.2147$).

Compared to solo howls, chorus howls had a significantly higher standard deviation of the mean frequency (`f0_StDv`) and a significantly larger frequency range (`freq_range`) in both test (test: $t(f_0_StDv) = 3.0431$, $p = 0.0139$; $t(\text{freq_range}) = 4.3202$, $p = 0.0019$) and control conditions (control: $t(f_0_StDv) = 2.8403$, $p = 0.0194$; $t(\text{freq_range}) = 2.9986$, $p = 0.0150$).

Solo howls had a higher minimum frequency (`f0_min`) than chorus howls, but the difference was significant only in the test ($t(f_0_min) = -3.0244$, $p = 0.0144$), and not in the control ($t(f_0_min) = -1.9825$, $p = 0.0787$) condition. Solo howls appeared to have a lower maximum frequency (`f0_max`) than chorus howls, but the difference was not significant (test: $t(f_0_max) = 1.4073$, $p = 0.1929$; control: $t(f_0_max) = 1.2040$, $p = 0.2593$).

Variation describes how much the pitch of a contour changes, whereas modulation describes how steep the slopes of pitch changes are. Solo howls seemed more modulated (co_mod) than chorus howls ($t(\text{co_mod}) = -1.1137$, $p = 0.2943$) in the test condition, while the opposite seemed to be true in the control condition ($t(\text{co_mod}) = 0.4698$, $p = 0.6497$), but neither effect was statistically significant. Solo howls varied (co_var) significantly less than chorus howls in both test and control conditions (test: $t(\text{co_var}) = 3.8126$, $p = 0.0041$; control: $t(\text{co_var}) = 3.2429$, $p = 0.0101$).

Table 6: Summary of the calculated paired t-test values per variable in the test and control conditions.

Test	T	Df	Tail	P-Val	95% Ci	Cohen-D	Bf10	Power
f ₀ _mean	-1.3349	9	Two-sided	0.2147	[-168.4, 43.41]	0.4215	0.62	0.2225
f ₀ _StDv	3.0431	9	Two-sided	0.0139*	[3.34, 21.18]	0.3978	4.75	0.1891
f ₀ _range	4.3202	9	Two-sided	0.0019*	[29.1, 93.08]	0.5827	23.65	0.3774
voc_length	3.2147	9	Two-sided	0.0106*	[0.38, 2.2]	1.5186	5.93	0.9889
f ₀ _min	-3.0244	9	Two-sided	0.0144*	[-77.39, -11.16]	0.8417	4.64	0.6598
f ₀ _max	1.4073	9	Two-sided	0.1929	[-10.21, 43.84]	0.1669	0.67	0.0761
co_var	3.8126	9	Two-sided	0.0041*	[1.48, 5.79]	0.5681	12.66	0.3619
co_mod	-1.1137	9	Two-sided	0.2943	[-0.1, 0.03]	0.4096	0.51	0.2128

Control	T	Df	Tail	P-Val	95% Ci	Cohen-D	Bf10	Power
f ₀ _mean	-1.3349	9	Two-sided	0.2147	[-168.4, 43.41]	0.4215	0.62	0.2225
f ₀ _StDv	2.8403	9	Two-sided	0.0194*	[2.32, 20.45]	0.3921	3.66	0.1989
f ₀ _range	2.9986	9	Two-sided	0.0150*	[11.69, 83.51]	0.4897	4.49	0.2833
voc_length	2.0688	9	Two-sided	0.0685	[-0.06, 1.43]	0.7964	1.39	0.6124
f ₀ _min	-1.9825	9	Two-sided	0.0787	[-68.25, 4.5]	0.5724	1.26	0.3664
f ₀ _max	1.2040	9	Two-sided	0.2593	[-13.82, 45.27]	0.1643	0.55	0.0753
co_var	3.2429	9	Two-sided	0.0101*	[1.07, 6.0]	0.5443	6.14	0.3373
co_mod	0.4698	9	Two-sided	0.6497	[-0.06, 0.1]	0.0877	0.34	0.0571

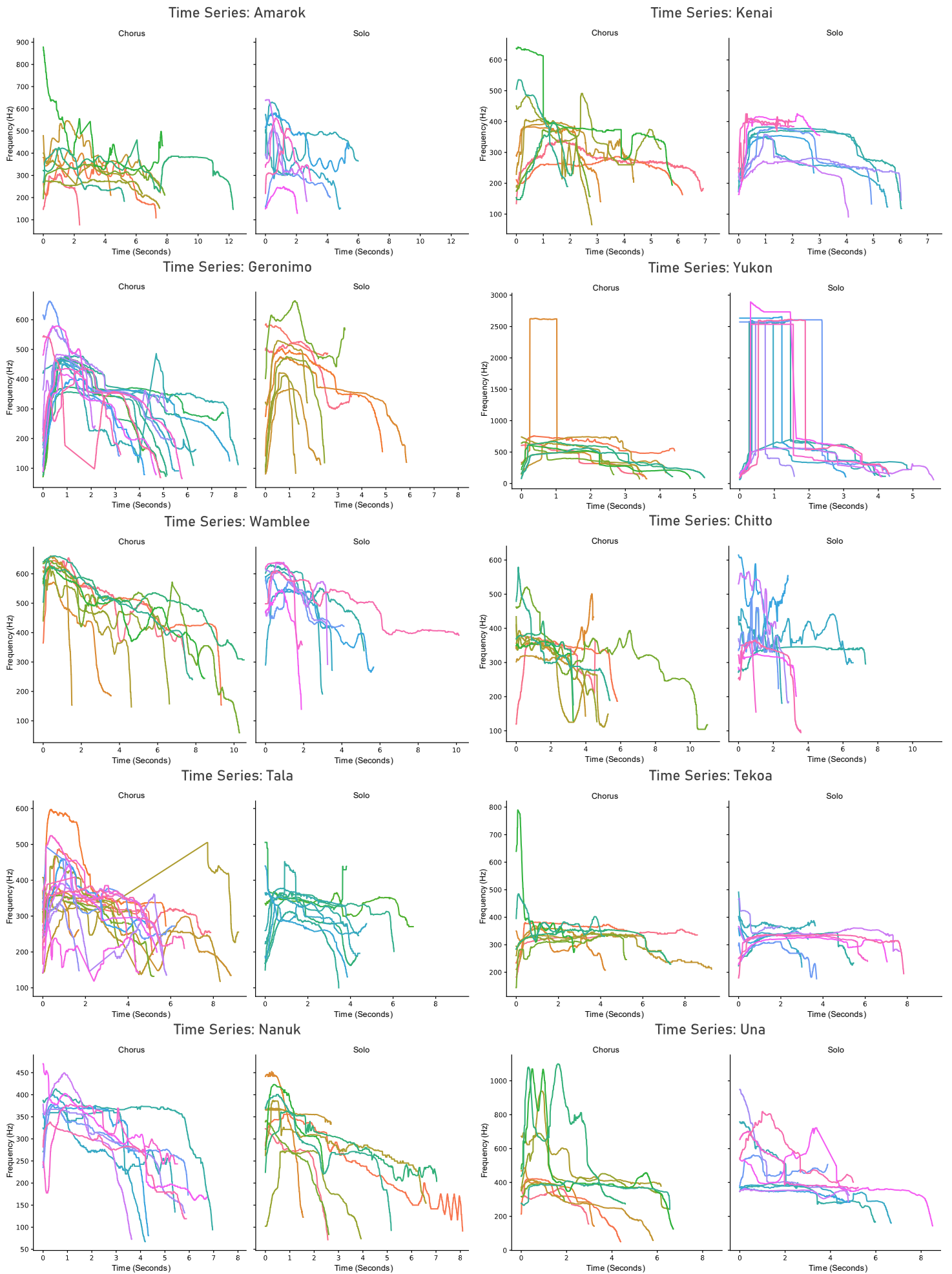


Figure 14: Time series comparisons of solo and chorus howls per individual.

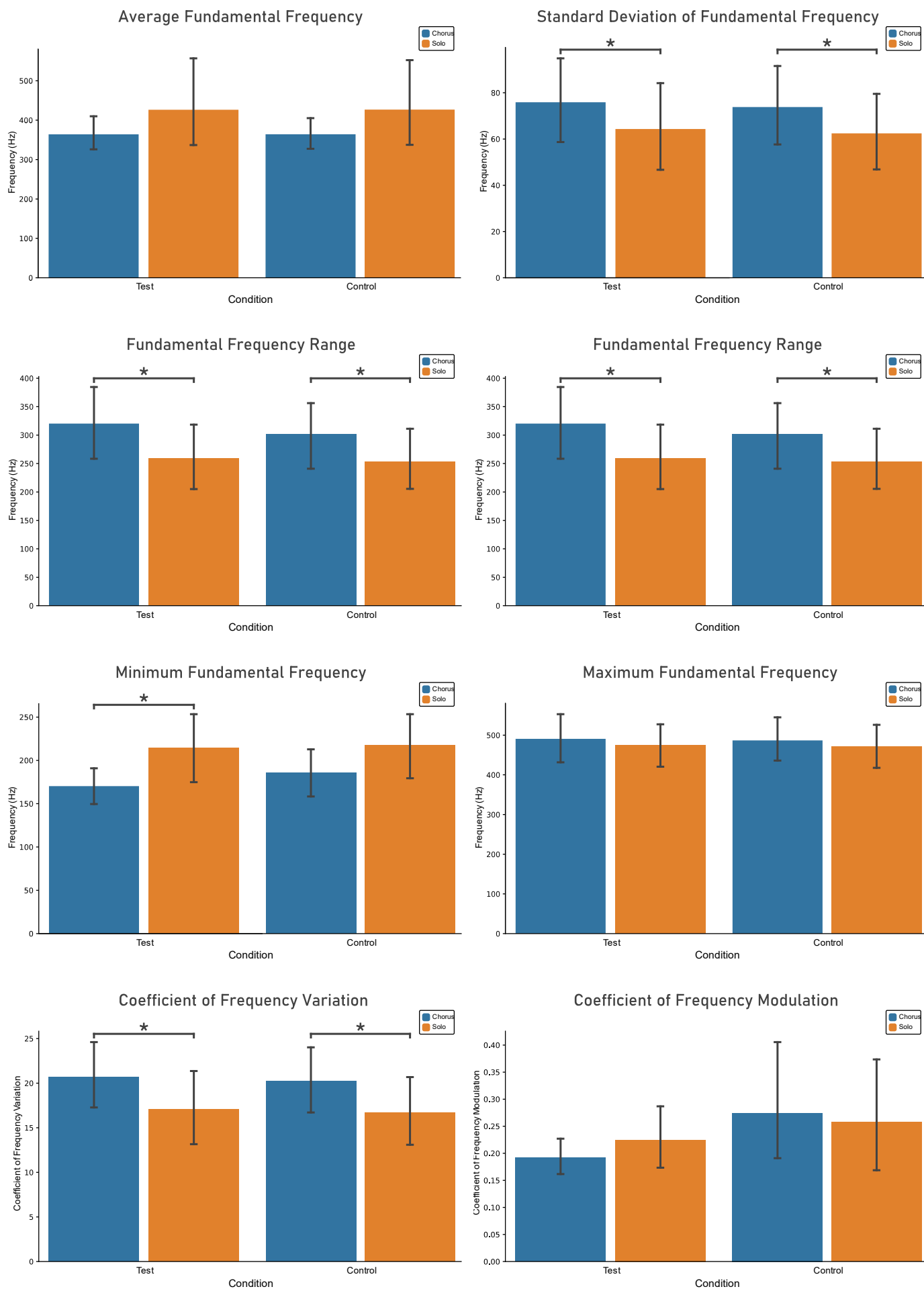


Figure 15: Bar plots for each variable in test and control conditions.

Discussion

This study aimed to investigate whether the acoustic structure of the howls of a population of captive timber wolves is influenced by a pack member howling concurrently. Analysing the fundamental frequency contours revealed significant differences in their standard deviation, frequency range, vocalisation length, minimum frequency, and frequency variation. Repeating these analyses after controlling for silences removed the significant effects from vocalisation length and minimum frequency, but left the significant effects of the standard deviation, the frequency range and the coefficient of variation. In short, our data suggests that the acoustic shapes of chorus howls are more varied and cover a greater frequency range than those of solo howls. The fact that we see these shifts despite not controlling for demographical factors or other contexts lends credibility to the idea that wolves flexibly adapt the acoustic features of their howls when they vocalise together with their packmates, i.e., individuals they are socially bonded with.

Solo Howls vs. Dyadic Howls

Something striking about our results is that the frequency range (defined as the difference between the maximum and minimum frequency) differs significantly in both the test and control condition (with effect sizes between 0.45 and 0.60). However, maximum frequencies are very consistent (i.e., they do not differ significantly between test and control conditions) and differences in minimum frequencies lose their statistical significance in the control condition, albeit barely. The latter is possibly a statistical artifact driven by how sub-vocalisations are created in the control condition.

Controlling for silences in chorus bouts where one individual howls for such a long time that the dyad partner can interject multiple shorter howls (what we call a sub-vocalisation) is necessary to avoid introducing undue bias. Otherwise, the sum of the multiple shorter howls and their silences would count as the total contour length. However, this should not be done for breaking howls in the future, as treating the parts before and after the break as actual sub-vocalisations unduly skews variables such as duration, minimum and maximum frequencies. For example, the first part of a breaking howl would be short, show generally little variation and a considerably lower maximum frequency. This might explain why, even though it is not statistically significant in either case, the coefficient of frequency modulation appears to reverse trends between test and control condition (see bar plot in Figure 15 on Page 24).

Howls tended to be longer during chorusing events, but unsurprisingly, controlling for silences resulted in the difference no longer being significant. Vocalisation length is a necessary and common variable in bioacoustics studies. However, silences or breaks in howls make it difficult to decide what counts as a “single” howl. Drawing lines between howls involves a significant amount of guesswork on part of the researcher, who needs to decide what is a break and what is not, as well as determine when a solo howl can be called as such, as we can never know when a howling pack mate (or even non-pack mate) stops influencing the inner state of a given focal individual. Technical limitations often require discarding very convoluted chorus bouts from analyses which also inevitably leads to information loss.

Our most important finding is the general variability of howls in solo and chorus conditions, represented by statistically significant differences in the howls’ standard deviation, frequency range and the coefficient of variation. This confirms our initial impressions of the time series cluster comparisons: fundamental frequency contours extracted from dyadic howls are more varied and use a greater range of frequencies than their solo howl counterparts.

Analysing the features of the howls’ fundamental frequencies is the most obvious and accessible approach to investigating the superficial difference between these long-distance calls in different contexts, but it does not tell us why these shifts happen. If we recall the chimpanzee pant-hoot example, where Mitani and Gros-Louis (1998) analysed long-distance calls of chorusing dyads, they hypothesised that chimpanzee males either produce more similar calls during chorusing because they share a common affective state, or because they actively match their calls to their partner. The fact that the acoustic features of our wolves’ howls trend in the same direction would speak for a common motivational state as the reason underpinning this phenomenon. Active call matching or convergence is also a possibility. We are working on a robust method to investigate this by artificially creating dyadic howls using the solo howl dataset and compare these artificial howls to natural dyadic howl contours.

Howls primarily serve two purposes: reassembly of separated pack members and maintaining distance to other packs (Harrington and Asa, 2003). Since the vast majority of our recordings were conducted while the pack was intact, I assume that most of these long-distance calls are directed at neighbouring packs, which are all well within earshot, but rarely within line of sight. Harrington (1989) observed that little useful information about pack size can be found in chorus howling, and that the structure of such howls might be a mammalian example of the Beau Geste effect. It would make sense for packs to appear as big (and thus competitive) as possible to other packs, and complex collective calling can certainly obfuscate or exaggerate the true number of pack mates. Conversely, solo howls have no need to advertise the whole pack, but rather transport individual information about the sender to a listening pack member or potential mate.

Individually recognisable features seem to be coded in how certain feature patterns emerge in a howl; a combination of, for example, modulation slopes, abrupt changes, frequency range, and amplitude changes (Palacios et al., 2007; Root-Gutteridge et al., 2014; Sadhukhan et al., 2021; Watson et al., 2018; Zaccaroni et al., 2012). Motivational states or audience effects can then let these patterns trend in a certain direction, as has been observed during aggressive interactions, where howls were noticeably lower and noisier (Harrington, 1987).

We decided to categorise our calls depending on whether a pack member was howling concurrently to the focal individual, but the WSC houses many packs in close proximity, whose composition is not a natural family unit, but artificially chosen and sometimes rearranged by staff. A focal individual might be listening and/or responding to siblings or former pack members that have been separated as adults, which our approach does not take into account. As such, our findings have limited applicability to wolves living in the wild.

Another noteworthy phenomenon is the fact that every single wolf at the WSC, no matter how timid and quiet otherwise, will howl for the Ernstbrunn firefighters' siren test that happens every Saturday at noon. It begs the question: what feature of this very artificial sound urges them all on so strongly that it seemingly trumps all other decision-making factors – its loudness, its characteristic swelling, or something else entirely? While one howling pack often leads to others joining in, it rarely results in a unison like that caused by the siren's sound. Could it be perceived as a threat, or does something else about the sound strongly arouse them? It would be interesting to present both individuals and groups with a range of acoustic stimuli to test whether such stimuli alone can elicit a howling response and if so, which acoustic features of the stimuli may cause the response.

Conclusion

Comparative biology is our strongest asset in the endeavour to tease apart the interplay between extant species' anatomy, (social) ecology, neurological capabilities, their vocal production, processing, and decision-making, and subsequently draw conclusions about how our own impressive aptitude for speech has evolved.

Our findings – combined with evidence showing individuality (Palacios et al., 2007; Root-Gutteridge et al., 2014; Sadhukhan et al., 2021; Watson et al., 2018; Zaccaroni et al., 2012), other context specific modifications such as separation and aggression howls (Harrington, 1987; Watson et al., 2018), and the significant role of social bonds for vocal decision-making (Mazzini et al., 2013) open the door for a more granular investigation of this emerging picture of the vocal complexity of timber wolves, which in turn can tell us more about the important role of flexible vocalisations in the lives of highly social species.

In the video footage I took for identification purposes during the recording sessions, wolves can be seen turning their heads in a certain direction or perking their ears up prior to howling, solo or otherwise. Often, adjacent packs will be howling before or after the focal pack vocalises. It was not possible for me to document the sequence of each pack and individual howling in my session. This would allow additional factors such as the sequence of howling activity on a pack and individual level, accompanying non-vocal behaviours like body posture, facial expression, interactions with other wolves before or after howl bouts and head-turning or ear perking to be considered. The resulting data could help provide better insight into the effects of motivational states (e.g., arousal after friendly or aggressive interactions) or circumstantial influences (like pack-response howling, separation of a pack member) on the acoustic features of howls and thus wolves' ability to flexibly shape their vocalisations according to changes in their socio-ecological environment.

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