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Master thesis

Acoustic location systems (ALS) as a tool for group density, territory and behavioural analysis of wild white-handed gibbons (*Hylobates lar*) in a Sumatran lowland rainforest

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Table of contents

Abstract

For conservation purposes, a species' spatial distribution as well as the density at which it occurs are important measures of interest. However, conventional monitoring methods may fail to efficiently collect this data on species that are difficult to detect visually or that live in areas difficult to access for human observers. A variety of animal species produce conspicuous acoustic signals that can be detected over long distances. Researchers can take advantage of this trait with passive acoustic monitoring (PAM). Acoustic location systems (ALS) are a form of PAM and are designed to enable precise localization of recorded sound events. So far, only few studies investigated practical applications of ALS under field conditions in terrestrial systems. This study aimed to explore the suitability of an ALS as a tool in population density and home range assessments of vocally active species, as well as its ability to collect data for behavioural studies.

For this study, 20 time-synchronized recording devices were installed in the lowland peat swamp rainforest of Suaq Balimbing, Sumatra, Indonesia, covering an area of 300 ha. Using a machine learning algorithm, "great calls" of female white-handed gibbons (*Hylobates lar*) were extracted from a total of 53 days of recordings from 5 am to 4 pm each, over a period of 9 months in 2017. Caller locations were triangulated, and individual calling females were identified using idiosyncrasies in the great call structure and the caller location.

15 individual females were identified that had their home range within or in close proximity to the research area. The group density of white-handed gibbons in Suaq Balimbing was 1.4 groups/km^2 and an average home range measured 0.63 km^2. This is the largest home range size reported for this species. Gibbons in Suaq produced on average 1.3 songs daily per individual that lasted 14.3 minutes on average. Fruit availability did not have an important effect on gibbon singing behaviour, neither did the number of neighbouring groups and the distance to them.

It was shown that ALS is a reliable tool for home range and population density studies of highly vocal species such as gibbons under field conditions. I hope that more studies will apply ALS to investigate other vocal species such as other gibbon species or birds. Findings from such studies will be beneficial for conservation management as well. On the analysis side, the development of a common framework for the processing and analysis of acoustic data would be desirable in order to make ALS more applicable for conservationists and ecologists with limited programming skills.

Zusammenfassung

Die räumliche Verteilung einer Art sowie die Populationsdichte sind wichtige Messgrössen für den Naturschutz. Herkömmliche Monitoringmethoden, die auf der visuellen Beobachtung von Arten beruhen, sind jedoch ineffizient bei der Anwendung auf Arten, die schwierig zu beobachten sind oder welche in Gebieten vorkommen, die für Forscher schwer erreichbar sind. Eine Vielzahl von Tierarten erzeugt auffällige akustische Signale, die über weite Strecken hörbar sind. Diese können sich Forscher zunutze machen mit passivem akustischem Monitoring (PAM). Eine Form des PAM sind akustische Lokalisationssysteme (ALS), welche eine präzise Lokalisierung aufgezeichneter akustischer Ereignisse ermöglichen. Jedoch wurden praktische Anwendungen eines ALS unter Feldbedingungen erst in wenigen Studien eingehend untersucht. Die vorliegende Studie bezweckte, die Eignung von ALS als Instrument zur Ermittlung von Populationsdichten und Aktionsräumen (Home Ranges) vokaler Arten sowie zum Sammeln von Verhaltensdaten zu untersuchen.

Für diese Studie wurden 20 zeitsynchronisierte Tonaufnahmegeräte im Sumpfregenwald von Suaq Balimbing, Sumatra, Indonesien, auf einer Fläche von 300 Hektar installiert. Unter Verwendung eines maschinellen Lernalgorithmus wurden aus Aufnahmen von insgesamt 53 Tagen, jeweils von 05:00 – 16:00 Uhr über einen Zeitraum von 9 Monaten im Jahr 2017 sogenannte „Great Calls" von weiblichen Weisshandgibbons (*Hylobates lar*) extrahiert. Die Standorte der rufenden Gibbonweibchen wurden trianguliert und die Identität der Gibbons anhand von individuellen Merkmalen in der Struktur ihrer Great Calls bestimmt.

15 Individuen konnten so identifiziert werden, welche ihren Aktionsraum innerhalb oder in der Nähe des Untersuchungsgebietes hatten. Die Dichte an Gruppen von Weisshandgibbons betrug 1.4 Gruppen pro km² und ein durchschnittlicher Aktionsraum mass 0.63 km². Dies ist der grösste Aktionsraum, der für diese Art berichtet wurde. Die Gibbonweibchen in Suaq produzierten im Durchschnitt 1.3 Gesänge pro Tag, welche durchschnittlich 14.3 Minuten dauerten. Die Menge an Früchten, die im Gebiet verfügbar war, hatte keinen Einfluss auf das Singverhalten der Gibbons; auch die Anzahl benachbarter Gruppen und die Distanz zu ihnen schien keinen Einfluss zu haben.

Es konnte aufgezeigt werden, dass ALS ein zuverlässiges Instrument ist zur Bestimmung der Aktionsräume und Populationsdichten von gut hörbaren Tierarten wie den Gibbons. Ich hoffe, dass diese Erkenntnisse das Monitoring von weiteren vokalen Tierarten antreiben werden. Solche Untersuchungen kämen auch dem Naturschutz zugute. Ausserdem wäre die Entwicklung einer einheitlichen Methodik zur Verarbeitung und Analyse akustischer Daten wünschenswert, um PAM und ALS auch Anwendern mit begrenzten Programmierkenntnissen zugänglich zu machen.

1. Introduction

Globally, biodiversity is declining at a rapid rate. Over the past four decades, a decline of 60% of vertebrate populations was measured. Habitat loss and degradation form the greatest threats to those populations (WWF, 2018). Therefore, an important component for the conservation of global vertebrate biodiversity is the protection and conservation of their habitats. For successful conservation management, knowledge on where populations occur and at which density, as well as knowledge about their requirements for their habitats and resources is crucial. This is why there is a big effort in monitoring wildlife populations to determine population densities and their spatial distribution. Next to frequently used monitoring methods like camera trapping, GPS tagging or visual surveys, in species that use and defend particular areas, territory advertisement signals can be used for gathering data on presence/absence or even abundance of members of a species in an area. This information can be converted into a density measure for population density estimates.

Home ranges are an important element of the spatial distribution of many species and influence how they interact with their environment. A home range is defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." (Burt, 1943). Where it is economical, animals develop the strategy to defend a part of their home range, restricting access to the resources for other individuals or neighbouring groups. Such a part of the home range that is defended against intruders is defined as a territory (Burt, 1943). Whether it is economical to defend a territory relies on the productivity, predictability and distribution of limiting resources (Powell, 2000). Territory holders can defend it through physical encounters and fight. However, fighting is energetically costly and includes the risk of injuries or even death. More often, animals use olfactory, visual or auditory signals to mark and advertise their territory (Powell, 2000).

Home range analyses require more detailed data than the abundance of a species in an area. To assess home ranges, the identity of the individuals or groups sampled must be known. Furthermore, the locations of each group or individual need to be tracked over a longer period to define which area is traversed by them during their normal activities. This can be done for example by directly following the individuals in the field, or by deploying tracking devices on the animals. Focal follows however require habituation of individuals or groups and usually many hours of field observations. GPS tracking is a good method to obtain locations of the study animal in a high temporal resolution but is restricted to animals of a certain minimum size where the tracking device is not restricting their normal activities, and to animals that can be captured to deploy the tracking device. Where these conditions are not given, other monitoring methods may be more applicable. A wide range of animal species navigate or communicate with conspecifics through acoustic signals. Such signals can often be heard over long distances and may contain information on species, individual identity, sex, age or context (e.g. Blumstein & Munos, 2005). Researchers have made use of these acoustic signals with passive acoustic monitoring (PAM, e.g. Depraetere et al., 2012; Suter et al., 2017).

1.1 Passive acoustic monitoring (PAM) and acoustic location systems (ALS)

Passive acoustic monitoring (PAM) is a method to obtain data using acoustic cues in the environment. It usually includes either human listeners or automated or non-automated audio recording devices. PAM was first widely used in the study of marine mammals (Watkins & Schevill, 1972; Gillespie, 2004; Mellinger et al., 2007), because sound waves propagate over long distances underwater while visibility is low. In the last decade, an increasing number of studies has applied acoustic monitoring methods also in terrestrial species including primates (e.g. Heinicke et al., 2015), birds (e.g. Mennill et al., 2006;

Bardeli et al., 2010; Frommolt, 2017), large carnivores (e.g. Comazzi et al., 2016; Suter et al., 2017), insects (e.g. Ganchev & Potamitis, 2007), and elephants (e.g. Thompson et al., 2010; Zeppelzauer, Hensman, & Stoeger, 2015). Automated PAM has been applied in various types of biological and ecological studies, be it the study of soundscapes of different ecosystems, often in connection with the diversity as well as 'healthiness' of its communities (Depraetere et al., 2012; Tucker et al., 2014; Burivalova et al., 2018), or as a tool for presence/absence monitoring or population density estimates of target species (Marques et al., 2013).

Over the last few years, new software has been developed, more affordable recording devices became available and computational and data storage capacities multiplied, which made acoustic methods with automated recording devices increasingly interesting and accessible to ecologists, conservationists and behavioral biologists. Combined with artificial intelligence and machine learning – a field that is rapidly evolving and increasingly finding applications in all fields of studies and everyday life – automated PAM has great potential to become a very useful and powerful tool in biological and ecological studies. Its advantages over human observer based PAM methods are obvious: By deploying multiple recording devices, a bigger continuous area can be monitored simultaneously. It also allows continuous monitoring efforts without disturbing the animals with the presence of humans and in areas that are too remote or dangerous to be accessed by human observers. Long-term and continuous data of an area becomes easier to collect, and vocal activities can be monitored even during the night. Furthermore, recorded sound data can be stored and is available for re-inspection (Sugai, Silva, Ribeiro, & Llusia, 2019).

Another benefit of PAM is the possibility to triangulate the location of the sound source with a suitable set up of the recording devices, a so-called Acoustic Location System (ALS). Triangulations of caller locations have also been done in human observer based acoustic surveys (O'Brien, et al., 2004; Kidney et al., 2016), an approach also referred to as "point counts" (Warren Y. Brockelman & Srikosamatara, 1993). However, there are a number of constraints to this method, as discussed by Rawson (2010). The main problems are the subjectivity of estimations of distance and bearing between observer and the heard call, detection probabilities being <1, inability to appropriately extrapolate population density estimations to a larger area than the one surveyed, and the lack of a robust method to distinguish different calling individuals. This means that despite a large sampling effort, the obtained data can still be inaccurate and misrepresentative.

ALS is able to overcome some of the above mentioned problems. Triangulation methods based on the time difference of arrival of an acoustic signal at time-synchronized recording devices offer an objective and more precise alternative to the triangulation methods in surveys with multiple human listeners. Furthermore, recordings from ALS open paths for more objective methods in determining the identity of calling individuals, since the calls can be stored and are available for comparisons and as reference for later analyses. Additionally, since an ALS can monitor an area over a greater temporal and spatial extent, there is potential to answer questions not only related to population densities, but also to the vocal and ranging behaviour of a local population as well as interactions between multiple calling individuals. A few studies have applied ALS on terrestrial species, such as Mennill et al. (2006) on rufous-and-white wrens (*Thryothorus rufalbus*), Collier, Kirschel et al. (2010) on Mexican Antthrush (*Formicarius moniliger*) and Spillmann et al. (2015) on Bornean orangutans (*Pongo pygmaeus*), but they mainly focused on assessing the localization accuracy of ALS. Despite its potential, the suitability of an ALS for population density estimates, home range analysis and studies on behavioural aspects has not been explored extensively in terrestrial systems (but see Collier, Blumstein, et al., 2010; Fitzsimmons et al., 2008; Spillmann, Willems, et al., 2017; Wrege et al., 2012). This is where this study here focuses on.

1.2 Gibbons as study species with ALS

The ideal study species to test the applicability of an acoustic location system for population density estimates, home range analyses and behavioural studies should be highly vocally active, have stable home ranges over the study period and should occur in densities high enough that a study area of suitable size can be covered in a financially and logistically achievable manner. Such a study species is the white-handed gibbon (*Hylobates lar*).

White-handed gibbons, also called lar gibbons, are a member of the gibbon family (Hylobatidae), the smallest of all apes. They inhabit the forests of South East Asia (Figure 1) and are known as highly vocally active animals. Their distinct long-distance calls – often referred to as songs – can be heard over distances up to 1 km in a forest habitat (Raemaekers et al., 1984) and serve as advertisement signals to defend their territory (Cowlishaw, 1992). Lar gibbons live in small family groups of 2-7 individuals, consisting of a monogamous mated pair and their offspring (Bartlett, 2003). They occupy highly stable home ranges over several years (Bartlett, Light, & Brockelman, 2016). Their diet is mainly frugivorous, but they also feed on leaves, flowers and insects (Bartlett, 2009; Bartlett, Light, & Brockelman, 2016). According to the IUCN Red List of Species, white-handed gibbons are endangered. In fact, 17 out of 18 gibbon species are endangered or critically endangered, the main threats being habitat loss and poaching (IUCN, 2008).

Figure 1: Current distribution of white-handed gibbons (Hylobates lar). (IUCN, 2008)

Their shyness and agility with which they move through the forest canopy makes it difficult to study gibbons in the wild. Therefore, studies on their ecology and behaviour which are a crucial basis for successful management and conservation actions generally require previous habituation of gibbon groups. The habituation of gibbon groups is a process that can take several months (Cheyne, 2010). Therefore, it is not surprising that the majority of scientific publications on the ecology and behaviour of wild white-handed gibbons originate from one well established long-term study site called Mo Singto in the Khao Yai National Park in Thailand (e.g. Reichard, 1998; Savini et al., 2008; Bartlett, Light, & Brockelman, 2016). Population densities and home range sizes were also assessed on populations in peninsular Malaysia and on the closely related species of Bornean agile gibbons (*Hylobates albibarbis*) (D. J. Chivers, 1979; 1984; Cheyne et al., 2008). However, there are big differences in population

densities and home range sizes between the study site in Thailand and those in Malaysia and Borneo. PAM and ALS could help shed light on these different findings by estimating population densities and home ranges from other field sites with still unhabituated gibbon groups.

1.3 Vocal behaviour of white-handed gibbons

Raemaekers et al. (1984) classified seven types of loud, long-distance call bouts produced by white-handed gibbons, which can be generally grouped into three categories: male solo songs, female solo songs and duet songs. These loud song bouts are species- and sex-specific. They fall within the frequency range of about 400 Hz up to 1600 Hz (Raemaekers et al., 1984).

Duet songs

Duet songs are only produced by mated pairs (Brockelman & Srikosamatara, 1993; Cowlishaw, 1992; Raemaekers et al., 1984) and serve as territorial defense and as advertisement of the mated pair status to conspecifics (Cowlishaw, 1992). They are given mostly in the morning hours after dawn and before noon, from any location in the gibbon territory (Raemaekers et al., 1984). These duet songs follow a clear structure that is consistent over most gibbon species: An introductory phase (Figure 2a), where both individuals produce a variety of short notes is followed by the so-called "great call" sequence (Figure 2b) produced by the female. Often, the female great call is followed by a short response from the male, the "coda" (Figure 2c). Then, both the female and the male engage in the interlude sequence, which is similar to the introductory sequence. Interlude and great call sequences are then given alternatingly for the rest of the song bout. Such a duet song bout lasts from about ten to thirty minutes (Raemaekers et al., 1984; Mitani, 1985).
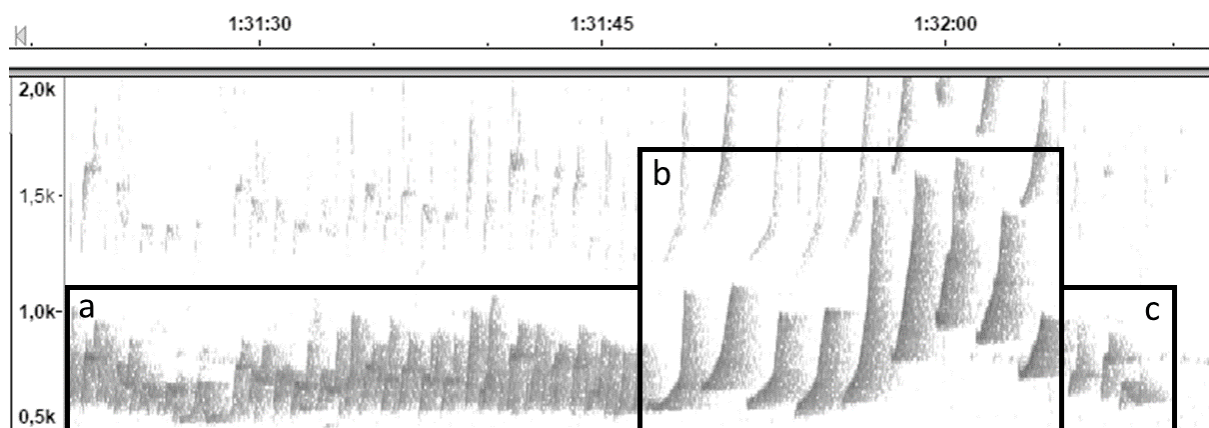

Figure 2: Excerpt of a white-handed gibbon duet song. a: introductory sequence, male and female participating; b: female great call, here composed of nine notes; c: male coda

Great calls

From all call types present in a duet song, the female's great call is the most stereotyped. It is only produced by females, lasts approximately 20 s and is made up of 6-13 notes (Raemaekers et al., 1984). It has a general two-humped shape, the first peak occurring after the first few notes rising up to ca. 1200 Hz, then falling lower in pitch again before reaching the climax at about 1300-1600 Hz and ultimately falling lower again. The exact number of notes varies within the same song produced by the individual, as well as between different individuals. However, the general shape of the great call is very

consistent within individuals and varies among individuals (Raemaekers et al., 1984). Most great calls analyzed in this study showed reoccurring shapes and structures that were characteristic for an individual. This complies with findings of Terleph et al. (2015) that individuality is encoded in the female great call of lar gibbons.

Great calls are not only produced in duet songs, but also as isolated great calls and in female solo songs by mated adult females, juveniles may join their mothers when singing (Raemaekers et al., 1984). Solitary females without an established home range do not sing, widows holding a home range, however, may sing occasionally (Leighton, 1987; Cowlishaw, 1992). Female solo songs have the same structure as the female's contribution to the duet song. Moreover, they provoked the same reactions as duet songs in both sexes during playback experiments. Therefore, it is concluded that the female solo song has the same territorial function as duet songs (Cowlishaw, 1992).

Due to its characteristics of a) being highly stereotyped and therefore easily detectable by listeners, b) being produced in a territorial defense context, c) encoding individual caller identity and d) being audible over long distances, the lar gibbon's female great call is a highly suitable call type for acoustic monitoring methods.

1.4 Research questions

In this study, I investigated an ALS as a potential tool to answer questions on territory locations and sizes, group densities and behaviour of a population of unhabituated wild white-handed gibbons in Suaq Balimbing, Sumatra, a site where no extensive gibbon studies have been carried out before. Finally, this study aims to give recommendations on the use of ALS as a monitoring method in the context of wildlife conservation.

What is the density of white-handed gibbon groups in Suaq Balimbing, Sumatra, Indonesia?

Lar gibbons were found at densities of <4.0 – 6.5 groups/km^2 in Khao Yai National Park, Thailand (D. J. Chivers, 1984) and 0.7-2 groups/km^2 at different sites in peninsular Malaysia (D. J. Chivers, 1979). The study site in Thailand is a tropical seasonal evergreen forest (Bartlett et al., 2016), whereas the forests in Malaysia are evergreen rainforests without distinct dry seasons (Chivers, 1980). The forests in Sumatra are evergreen rainforests as well, so that the group density in Suaq Balimbing might resemble the ones in Malaysia. It is important to note that Suaq Balimbing lies in a peat swamp rainforest. A study on Bornean agile gibbons (*Hylobates albibarbis*) carried out in a similar peat swamp forest habitat resulted in 2.6 groups/km^2 (Cheyne et al., 2008). A similar density is therefore expected for Suaq Balimbing.

Where and how big are the territories of white-handed gibbons in Suaq Balimbing?

White-handed gibbons are territorial and maintain relatively small but stable home ranges across years (Bartlett, Light, & Brockelman, 2016). The gibbons of the well-studied population at Mo Singto in Thailand are known to have exceptionally small and highly overlapping home ranges of 0.24 km^2 and 64% overlap on average (Reichard & Sommer, 1997). Gibbons from Khlong Sai study area in the same Khao Yai National Park in Thailand had mean home range sizes of 0.31 km^2 with 6.9% overlap. Larger home ranges are reported from study sites on peninsular Malaysia (0.57 km^2, D. J. Chivers, 1984) and Sabangau catchment area on Borneo (0.53 km^2 with only 15% overlap, Cheyne et al., 2008). It is important to note that the method used in this study here relies on the territorial great call to pinpoint gibbon location, the derived area of gibbon activity should therefore correspond to a territory rather than a home range. Leighton (1987) reported that gibbon territories, defined as the area used

exclusively by one group and defended against neighbouring groups, made up 75% of the home range of a group. Although this value is likely to differ among different gibbon species and populations, I am using it here as an approximation for the conversion from territory to home range sizes. Therefore, I am expecting the territory sizes of gibbons in Suaq Balimbing to be in the range of 0.30-0.45 km^2.

How is gibbon calling behaviour influenced by territory intrusion pressure and fruit availability?

Since the examined great calls are given in a territorial defense context, it is expected that the singing intensity such as the rate at which calls are given, the duration of a song bout or the number of song bouts produced on a given day is enhanced with higher perceived or actual intrusion pressure by neighbouring groups (measured as the number of neighbouring groups and the distance to them). On the other hand, singing is energetically costly. In times when food is abundant, more energy can be allocated to singing behaviour. Therefore, I expect that fruit availability has a positive effect on singing intensity, represented in a higher great call rate, longer song duration and higher number of song bouts per day.

In order to test the hypotheses stated above, sound recordings from an ALS were analyzed. The collected raw sound data was first processed in these three main steps:

1) *Gibbon great-call detection:* using a machine-learning approach based on CNN (convolutional neural networks) and MFCC (Mel-frequency cepstral coefficients) as input features.
2) *Triangulation of caller location:* making use of the TDOA (time difference of arrival) of the sound signals at time-synchronized recording units
3) *Caller identification:* discriminating individual female gibbons by idiosyncrasies found in their great call structure and by taking into account the spatial information

The data resulting from these main processing steps was then used to build statistical models on the gibbons' calling behaviour and to assess group densities and the extent of their territories.

2. Materials and methods

2.1 Study area

The gibbon calls analyzed in this study were recorded in Suaq Balimbing (N03°02.873, E97°25.013), a research station managed by the Department of Anthropology of the University of Zurich. The tropical lowland peat swamp forest of Suaq Balimbing is located in the southwest of the Indonesian province of Aceh on the island of Sumatra (Figure 3). It lies within the Leuser Ecosystem, one of the world's most biodiverse landscapes, that is home to wild orangutans, elephants, tigers, rhinos and sun bears and a number of endemic species. The study area covers approximately 7 km^2 and stretches from the shore of the Lembang river up to ca. 2.5 km inland within the Gunung Leuser National Park to the foot of a hill. Being a peat swamp rainforest, the forest floor is almost permanently covered with water.

Figure 3: left: Location of Suaq Balimbing research station (Google Maps); right: Suaq Balimbing peat swamp rainforest

2.2 Data collection

In this study, audio recordings from 24th January – 15th September 2017 were used. The data on the white-handed gibbons in Suaq Balimbing was derived only from acoustic recordings. No additional data on behaviour, social structure or identity was collected by field observations, DNA sampling or other methods.

Audio field recordings in Suaq Balimbing were made by Brigitte Spillmann from October 2016 to January 2018, analogous to the method described in Spillmann et al. (2015). 16 Song Meter SM2+ and 4 Song Meter SM3 recording units (Wildlife Acoustics Inc.) were installed in a grid set up (Figure 4). The recorders were spaced out over an area of 3 km^2 in 500 m intervals. All recorders (Figure 14, Appendix I) were time-synchronized and the exact location determined via GPS. Each recorder was powered by a 12 V, 18 Ah dry gel battery which was charged by a 50 W solar panel. An omni-directional, weatherproof SMX-II microphone was connected to each of the recorders, placed at ca. 10m height in the canopy. Sample rate of the recordings was set at 22'050 Hz and the sample size was 16-bit (signed PCM). Sound files were saved on conventional SD cards (16 GB and 32 GB memory) in .wac file format

and copied onto an external hard drive during monthly recorder checks. They were then later converted into .wav files and uploaded onto a server.
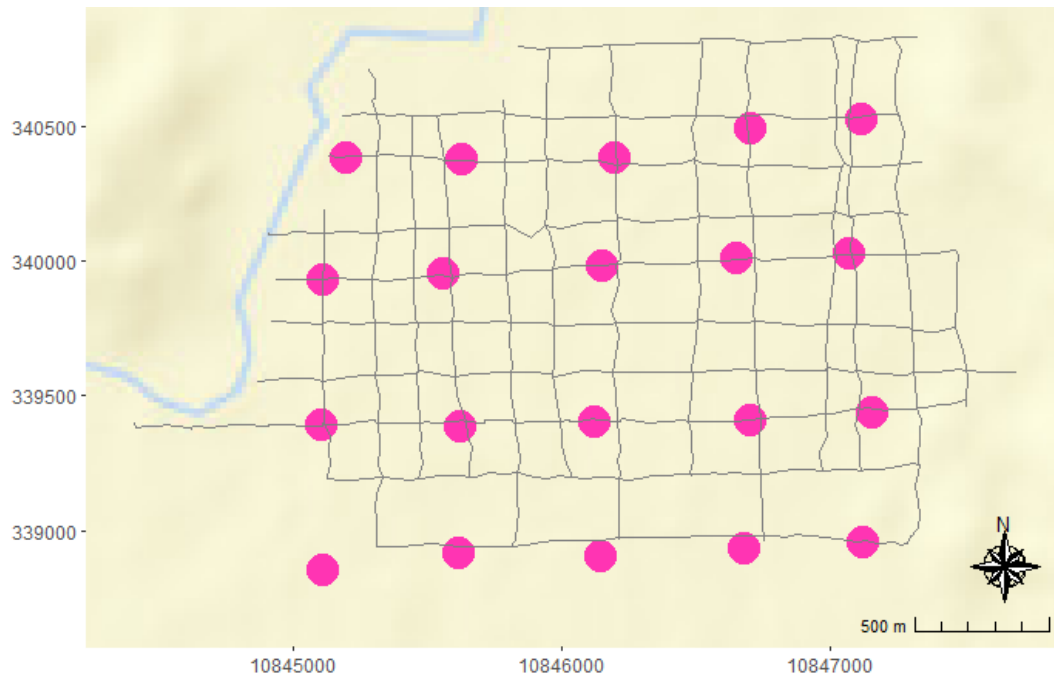

Figure 4: Map of the study area in Suaq Balimbing. Grey lines show the trail system. Red dots indicate locations of the 20 recording units. Distances between neighboring recorders are approximately 500 m. (Background map: ESRI)

Each recorder was programmed to record daily from 5 am to 7 pm, based on activity times of orangutans, (the original purpose of the recordings was to monitor orangutan calling activity), producing 7 daily recording files of 1 h 57 min length each ("track"). Three minutes between two consecutive tracks allowed enough time to save the file and to start a new recording. Starting times of the 20 recorders were staggered to ensure that a minimum of 15 recorders were running at all times during the day. Gaps occurred in the audio data on days where recorders were malfunctioning or had to be maintained (Figure 5). For 7% of the recorded tracks, the built-in GPS of the recording device was inactive. Such recordings could not be used for later triangulation of the call location. Nonetheless, a total of more than 100'000 hours worth of audio data was recorded over the entire recording period, out of which approximately 11'660 recording hours were used in this study.
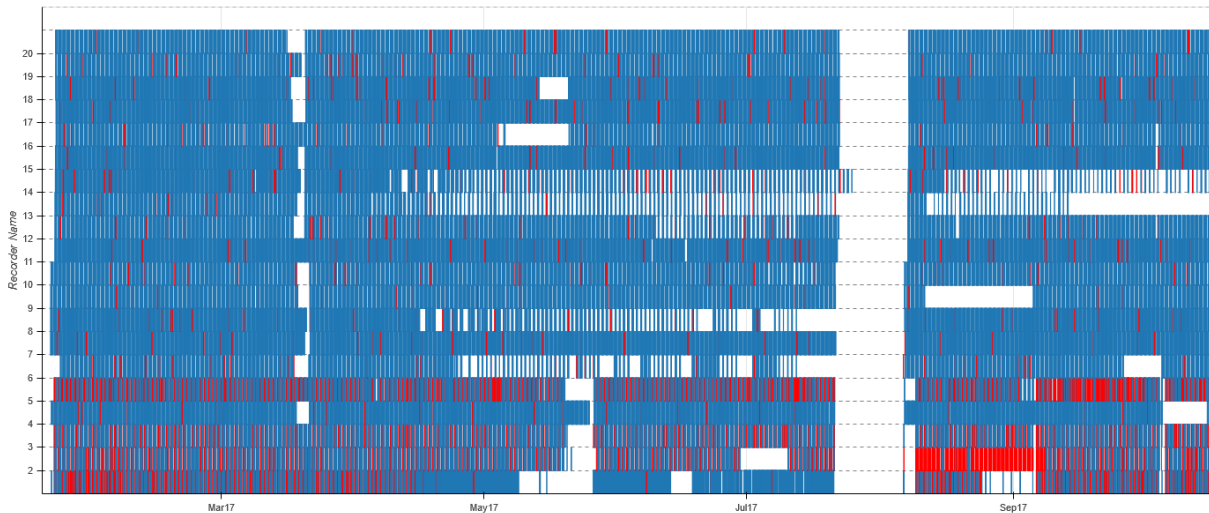
Figure 5: Overview of available recording tracks, from January 2017 to October 2018 (time on x-axis). Each horizontal row represents one of the 20 recorders. Blue bar: available sound track; red bar: available sound track without GPS signal (not usable for triangulation); white gaps: no recording available.
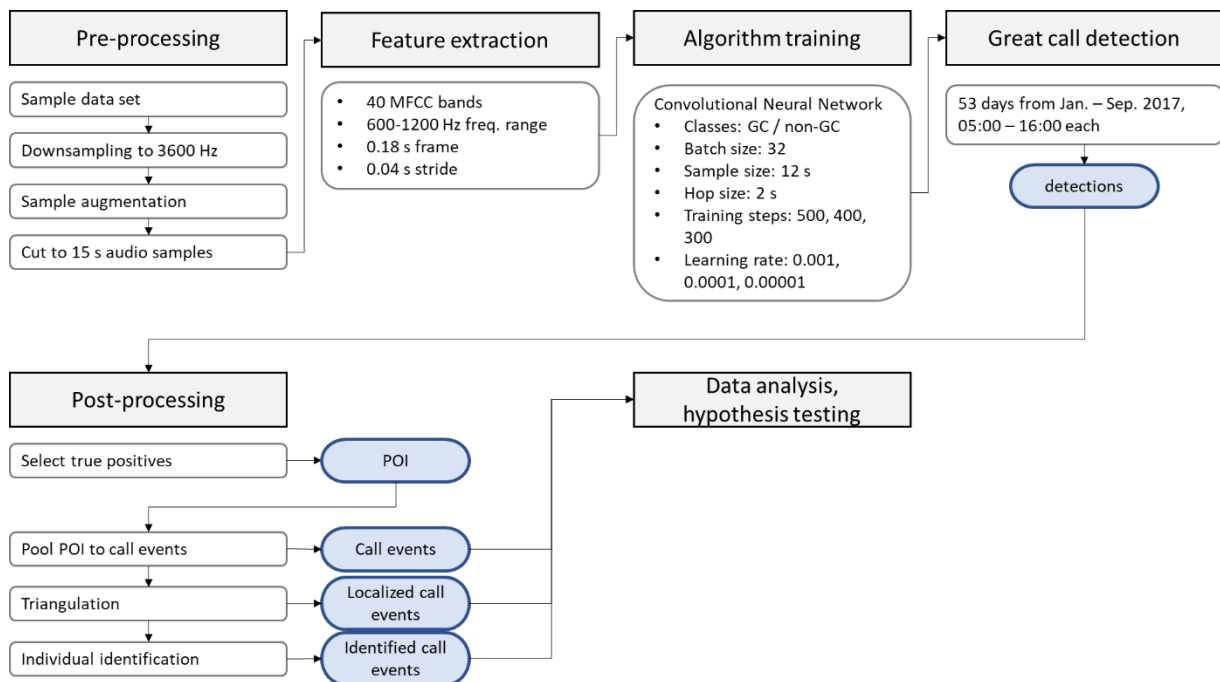
2.3 Data processing

Figure 6: Data processing consisted of the steps to develop and apply a gibbon great call detection algorithm (pre-processing, feature extraction, algorithm training and call detection) and post-processing, including the important steps of triangulation of caller locations and individual caller identification. The derived data was used for further analysis and hypothesis testing.

Gibbon great call detection

A machine learning approach was used to detect the female gibbons' great calls in the sound recordings, namely a Convolutional Neural Network (CNN). As input features for the CNN, Mel-Frequency Cepstral Coefficients (MFCC) were used. MFCC are commonly used in speech recognition

13

tasks and are based on the representation of sound on a logarithmic scale, approximating human perception of sound. A number of studies have applied MFCC features successfully in species and individual identification tasks in birds (Fox et al., 2008; Cheng et al., 2012), frogs (Lee et al., 2006; Ting Yuan & Athiar Ramli, 2013) and primates (Mielke & Zuberbühler, 2013; Spillmann et al., 2017; Clink et al., 2019). The use of MFCC features in sound classification tasks has several advantages over conventional measurements of acoustic parameters (Mielke & Zuberbühler, 2013). It does not rely on the researcher to choose relevant spectral parameters, and thus may pick up features that would not be obvious to a researcher but still be relevant for the recognition task. And importantly, MFCC feature extraction is fully automated and thus very fast.

During the pre-processing phase, the training data for the detection algorithm was collected from the original sound recordings. Training data consisted of two classes: a) gibbon great calls and b) non-gibbon great calls. The latter class included gibbon calls other than great calls, calls of other animals in the same frequency range as gibbon calls (mainly birds and frogs), male orangutan long calls, people talking and singing, background noise such as rain, wind, anthropogenic sounds and noises produced by the recording devices themselves. The initial set of training data comprised of 1'105 samples of gibbon great calls and 3'932 samples of other sounds. The training data was down sampled from a sample rate of 22050 Hz to 3600 Hz to reduce the file size and allow faster computation of the subsequent steps. Then the data set was split into a training dataset (70% of samples) and an evaluation dataset (30% of samples). The training dataset was further augmented in two steps by stretching or compressing the audio data by up to 0.01 seconds and then cutting samples of >15 seconds into several 15-second frames. Training of the detection algorithm was based on the resulting 12'648 gibbon great call samples and 16'518 samples of non-great call sounds.

MFCC feature extraction and training of the CNN was programmed by Raphael Walker using python programming language and Google's TensorFlow tool. 40 MFCC filterbanks were used to extract MFCC features in the frequency range of 600-1200 Hz. Restricting the frequency range here helps to avoid having high- and low-frequency noises in the training features (e.g. birds, cicadas) and to focus on the relevant range where gibbon great calls are produced. Settings for CNN training are shown in Figure 6.

After successful training, the detection algorithm scanned field recordings from 5-9 consecutive days of each month between January – September 2017, 53 days in total (Table 1). The days were chosen by the amount of quality data available for analysis after visual inspection of the track overview shown in Figure 5 (blue tracks). Only sound recordings from 05:00-16:00 were analyzed, corresponding to the general times of the day when white-handed gibbons are active (Reichard, 1998).

Table 1: Dates and number of days analyzed per month.

Month	Dates analyzed	Number of days analyzed
January 2017	24.-31.	8
February 2017	09.-13.	5
March 2017	22.-26.	5
April 2017	02.-06. + 15.	6
May 2017	27.-31.	5
June 2017	04.-08.	5
July 2017	12.-20.	9
August 2017	09.-13.	5
September 2017	11.-15.	5

The resulting great call detections by the algorithm were then inspected each manually to confirm whether it is a gibbon great call (true positive) or a false positive detection. Confirmed true positive detections became points of interest (POI), and all POI occurring within the same 20 seconds were grouped together into call events with a unique call ID.

The algorithm was kept generous with the number of false positive detections to minimize the number of missed great calls (false negatives). On average, the ratio of true positives to false positives was 1:2.6. Despite the additional step to manually select true positive detections, this process is substantially faster than scanning through the same amount of audio data and labeling target calls manually. Validation of the number of false negatives (present but not detected great calls) was done by manually labeling great calls from the recordings from two days (22 day hours or 427.05 recording hours), and comparing to the results of the detection algorithm (Appendix I, Table 8). Although the false negative rate on POI level was high with 41.6% (338/813), the algorithm did still detect 82.9% (155/187) of all great call events and 100% of the great call events within the recorder grid. As long as at least one POI of the same call event was picked up by the algorithm, the call event was registered. Additional POI of the same call event were easily found during post-processing. With this validation, I am confident to have detected practically all of the great call events from within the recorder grid.

Call source localization

The location of the detected call events in the study area could be computed if the call event was recorded on a minimum of three different recorders. To this mean, the time difference of arrival (TDOA) of the acoustic signal at the different recording units was obtained by cross-correlating the POI of the same call event. The TDOA between each recorder pair produced a hyperbola of all possible call source location. The intersection of two or more of these hyperbolae is the call source location. Hourly mean air temperatures, measured directly by each recording device, were accounted for when computing the cross-correlation.

In a forest environment, sound waves are diffracted at different trees and obstacles between sound source and receiver, leading to small differences of TDOA compared to sound traveling on a direct path in an open area. This can result in inaccuracies of the computed sound source locations. Based on the assumption that gibbons do not change their location while engaging in a song bout (T. Geissmann, pers. comm.), mean coordinates of each song bout were calculated from the coordinates of all great calls belonging to this same song bout. The deviation of each great call location from its mean song bout location was then calculated to assess localization error. In general, calls given from outside the recorder grid had higher inaccuracies. The mean deviation from song mean coordinates was 44.5m (SD ±50.9m) for all great calls given from within the boundaries of the recorder grid. Mean deviation was still acceptably low with 52.2m (SD ±54.7m) for all great calls given from maximum 200m outside the recorder grid. This complies with the findings of Spillmann et al. (2015), where the same ALS set up was used for the localization of male Bornean orangutan calls that have a similar reach as gibbon great calls. Therefore, for all analyses containing coordinate information, only localized calls at maximum 200m outside the recorder grid boundaries were used. This area is here referred to as the 'localization area'.

Caller identification

To be able to ultimately estimate gibbon group densities and territory sizes, different calling groups needed to be identified. All previous studies using automated individual recognition of animals by their calls had a set of recording samples from identified individuals as reference (Fox et al., 2008; Mielke &

Zuberbühler, 2013; Terleph et al., 2015; Clink et al., 2019). However, this was not the case in this study and a different approach had to be developed.

Since gibbons are territorial animals and keep their home ranges over several years (Bartlett et al., 2016), the location from where a call was given provided a first hint on the identity of the calling individual. Two calls given from locations >800 m away were unlikely to be from the same individual. This cue was combined with another approach, distinguishing individuals by the great call structure and characterizing them by idiosyncrasies. For this, the Fast Fourier transformed (FFT) spectrogram of each great call was examined visually, characteristic patterns in the great call structures identified and compared to other great calls. In this process, an identification catalogue was established as a reference (Appendix II). Apart from differences in the general temporal and spectral characteristics of the great call sequence (call duration, number of notes, frequency range), the second note of the great call (usually falling together with the first peak note of the call) showed distinct recognizable characteristics in shape and frequency range for the majority of calls. These individual characteristics were stable within the same call bout as well as across different days for the majority of calls. With this method, 15 individual females were identified living within or adjacent to the study area in hearing distance.

To test the reliability of this idiosyncrasies-based identification method, 550 identified call samples were used to train and to test a Gaussian mixture model (GMM) in MATLAB. GMM was already successfully applied in various studies on human speech recognition and in a caller identification task with male orangutan long-calls (Spillmann, van Schaik, et al., 2017). The call samples were shuffled into five different training data sets (each containing 80% of each individual's calls) and five test data sets (20% of each individual's calls). The second note of each call was isolated and the MFCC features extracted (12 filterbanks, frequency range 450-1500 Hz) to train the GMM. Due to constraints in the number of samples in sufficient quality, only 10 out of 15 identified individuals could be tested. The probability to correctly assign the individuals was 10% by pure chance. The GMM correctly identified the callers in 70.2% of the cases, thus performing seven times better than by chance. From this I conclude that the identification method using location information and idiosyncrasies in great call structure is meaningful.

The social status of the identified females – whether they are solitary or mated – was assessed by listening to their song bouts. If a female engaged in a duet song bout, she was classified as an adult mated female. A female that only produced solo song bouts but sang from a similar part of the study area was suspected to be a widowed individual that still holds a territory, based on the descriptions by Leighton (1987). Solitary females without a territory are not known to produce any solo songs (Leighton, 1987; Cowlishaw, 1992) and therefore would not be detected with acoustic monitoring.

Acoustic platform
Gibbon great call detection, call source localization as well as general access and display of the audio data stored on a server was facilitated by an acoustic platform. The acoustic platform was developed by Raphael Walker and Brigitte Spillmann and could be accessed via an online front end. It allowed accessing and processing a large amount of acoustic data in an efficient, organized way:

The great call detection algorithm could be directly applied on a selected range of audio data. For each detection, details such as start time and recorder ID were listed together with a spectrogram, so that true positive detections could easily be selected. Selected true positive detections were saved as individual POI and pooled together to call events. POI, call events and entire audio tracks could individually be accessed, downloaded for local storage and their spectrograms displayed. Furthermore,

call lists could be downloaded as a csv file containing details to each call event such as call ID, start and end time, coordinates, identification labels etc.

For the calculation of call locations, POIs could manually be deactivated to ensure correct localization. This was useful when not all POI were of good sound quality, e.g. with high background noise. The way the localization function was implemented was that a grid with 10x10m cells was superimposed to the map of the study area. After computing hyperbola from the time differences between pairs of recorders, the coordinates of the cell closest to the intersection point of the hyperbola was assigned as the coordinates of the call.

Fruit availability

Data on forest phenology was obtained from the Suaq Balimbing Research Station. Around the 15th of each month, 1'000 trees along two transects in the study area were inspected and the amount of young leaves, flowers, total fruits and ripe fruits were noted for each tree. The monthly fruit availability index (FAI) was calculated from this data and denotes the percentage of trees bearing fruits. Fruit availability ranged between 8.1% and 16.6% for the entire year of 2017 (Figure 7).
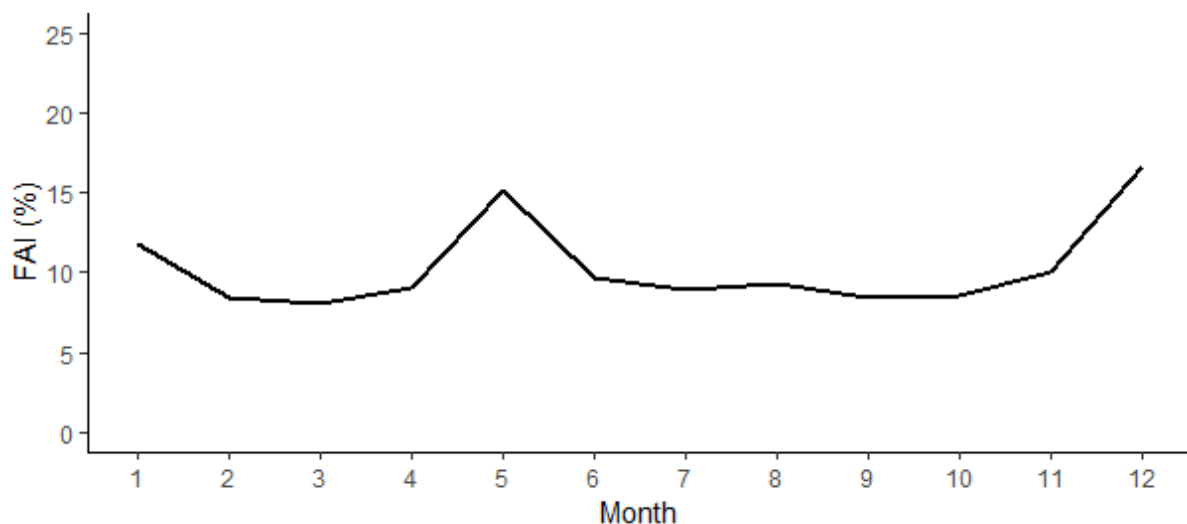

Figure 7: Fruit availability index measured in Suaq Balimbing for each month in 2017. Mean: 10.3%, min: 8.1%, max: 16.6%. FAI values from January to September were used in the analysis.

2.4 Data analysis

All analyses were done using R programming language Version 3.5.1 (R Core Team, 2018) and R Studio Version 1.1.423 (© 2009-2018 RStudio, Inc). Table 2 shows the definition of terms and variables used in the analysis.

Table 2: Definitions of variables and terms used in the analysis.

Song	A sequence of at least two great calls of an individual with time gaps not greater than 10 minutes between consecutive great calls.
Song duration	The time difference in seconds between start of the first great call of a song and start of the last great call of the same song.
Great call rate	The rate at which great calls were given in a song, in great calls per minute. Great call rate = (number of great calls – 1) / song duration * 60 seconds
Song mean coordinates	Mean coordinates calculated from coordinates of all great calls belonging to this same song.
Response song	The first song following another individual's song no longer than 30 minutes after the start of that song and not more than 500m away from the other individual's mean song location.
Audible song	The first song following another individual's song no longer than 30 minutes after the start of that song and not more than 1000m away (can be the same as a response song). This is based on the statement that gibbon songs are audible over ca. 1 km (Raemaekers et al., 1984).
Number of neighbours	The daily number of neighbours was determined as the number of groups that were singing in hearing distance (1000m) of the focal group on a given day. For this, the daily mean location of each singing group was calculated from the mean coordinates of each recorded song bout of a group.

Group Density and Territory Analysis

Using each song's mean coordinates and caller identity, 95% minimum convex polygons (MCP) were calculated as the gibbons' territories. This was done with the functions provided in the R package adehabitatHR (Calenge, 2006). Although kernel utilization densities (KUD) and Brownian bridges (BB) are more sophisticated methods for home range analyses (Powell, 2000), the simpler MCP method was considered to be better suitable for the sparse temporal resolution of relocations in this study. Because each song bout led to one location registered, there were only few location data points per day for any of the groups. Both KUD and BB highly overestimated the extent of the gibbon territories to areas where no great call of a particular individual was found. KUD and BB methods also resulted in highly overlapping polygons, which are untypical for the territorial gibbons.

Only data points from maximum 200m outside the recorder grid were used, due to localization inaccuracies for call locations further out. This means that territory sizes for groups at the edge of the study area were not adequate and only represented a part of their real territory.

The gibbon group density in Suaq Balimbing was determined as the number of groups resident within the study area divided by the size of the localization area (5 km^2). As residents, groups were counted that had a majority (>50%) of all their songs localized within the localization area and that were

detected on more than 17 days (>33% of days analyzed). Since there is no information on the group size of in the study area, the density estimation can only be made on group level.

Influence of territory intrusion pressure and fruit availability on singing intensity
Statistical analyses of the gibbons' singing behaviour were first done on day level where songs from all individuals were aggregated, and then on individual level where for each day, the songs of different individuals were grouped separately. Two days where it was raining heavily (28.01.2017 and 15.04.2017) were excluded from this analysis, because the rain might have influenced the detection rate of great calls on these days, which affects the calculated call rates and song durations.

On day level, the hypotheses on gibbon calling behaviour were tested with linear models (LM) and generalized linear models (GLM). I tested whether fruit availability and the number of groups singing on that day have an influence on the total number of songs produced, the mean song duration and the mean great call rate.

Hypothesis testing on individual level was done using linear mixed-effects models (LME) and generalized linear mixed-effects models (GLME) in the R package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017). Different models were built where the singing intensity was represented by the response variables number of songs given, mean song duration and mean great call rate. Fixed variables were fruit availability, the number of neighbours, and if a song classified as a response (n=23) or audible song (n=57) (Table 2), the distance to the song to which the individual responded and the distance to the song to which the individual was in hearing distance. All models on individual level contained the individual as random effect.

To test whether response variables differed significantly between individuals, ANOVA (for continuous data) and Kruskal-Wallis tests (for count data) were used. Models on individual level were built only for response variables that differed significantly between individuals. For each response variable, the model with the lowest AIC value was selected as the best fitting model.

3. Results

3.1 Gibbon great call detection and call source localization

Running the great call detection algorithm was substantially faster than scanning all audio files visually. It took about 1.5 h – 2 h to run the detection task for one recording day (approximately 132 recording hours = 11 hours * 20 recorders), while manual labeling took about 5 min per 2 h recording, adding up to 5.5 h for 132 recording hours (and this was purely for labeling the calls, without any cutting and separate storage of the detected calls). A day worth of recordings resulted in 194-584 detections. The number of detections and especially the ratio of true positives to false positives was highly variable and seemed to be highly affected by weather conditions as well as human activities in the forest. High background noise levels from rain, wind and chainsaw sounds often led to false positive detections only containing noise. The sound of talking people in the forest was also often confused as great calls by the algorithm. The average ratio of true positive detections to false positive detections was 1.4 (range 0.1-25.8) per recording day.

From the 53 days analyzed over the study period of 9 months, 3352 great call events were detected. 47.8% (1601) of all detected great call events could be localized, 37.9% of the call events (1271) were given from inside the defined localization area. For 85.7% (2871) of all detected great calls, the calling individual could be identified. Calls that could not be identified were of low quality (signal too weak), were overlapped by noise from other animals or human activity (chainsaw noise) or the call structure did not match clearly with the characteristics of one of the identified individuals. The detected calls belonged to a total of 465 song bouts (containing >1 great call) given by identified individuals, which means that on average, 8.8 song bouts were detected on each survey day. 317 (68.2%) songs could be localized, 279 (60.0%) of them were located within the localization area.

The heat map in Figure 8 shows the distribution of all localized great call events within the localization area. It becomes obvious that there are areas where gibbon singing activity was very low, and areas in the south and north east end of the study area that had high singing activities.
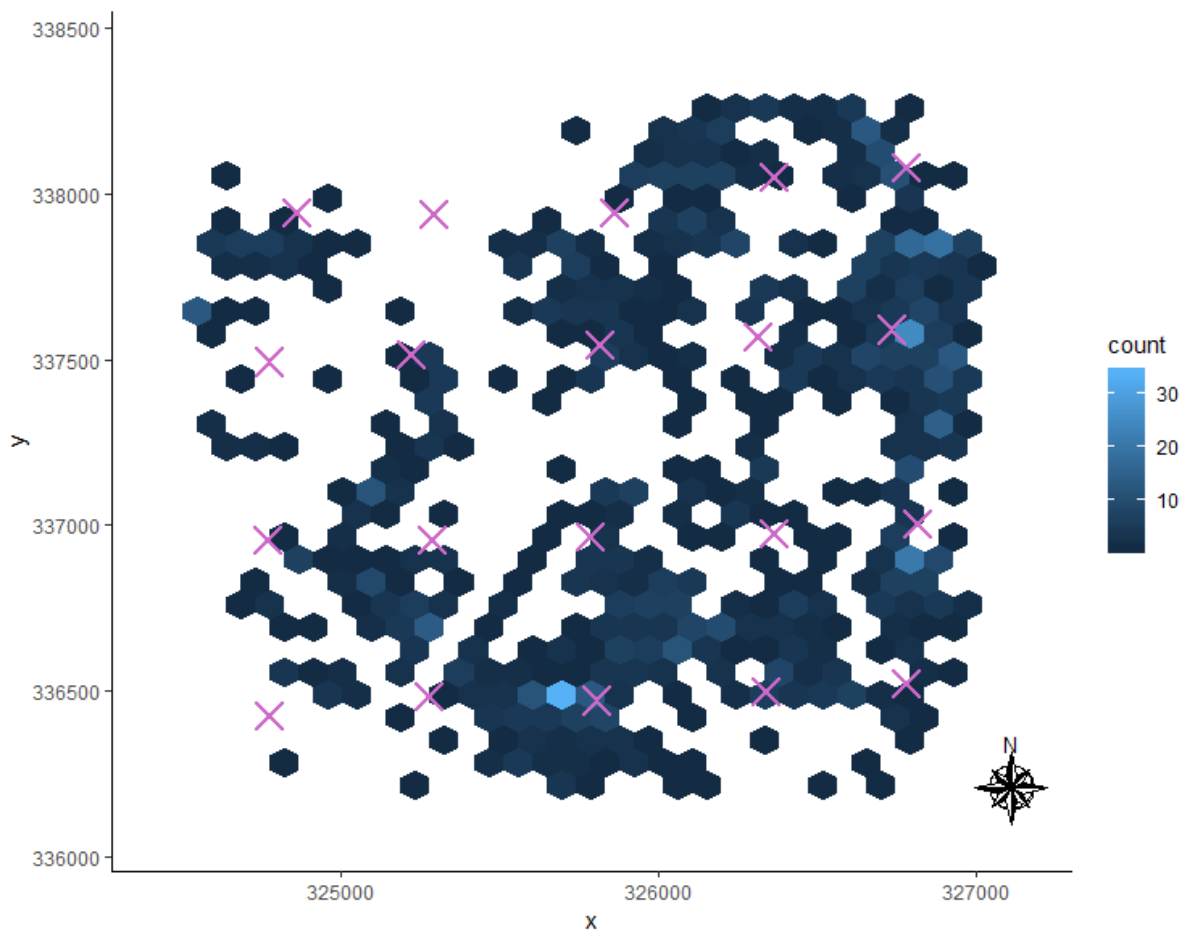
Figure 8: Heat map representation of gibbon great call activity. Purple x's mark locations of recorders.

3.2 Group density and territory analysis

Group density

During the entire study period from January 2017 – September 2017, 15 females were identified and given individual names (see Table 3). With the exception of two females Jolli and Ximena, all females engaged in duet songs, from which we can conclude that they are adult mated females. Jolli was only found in solo songs, and also sang on only 10 out of 53 days surveyed but always sang from a similar region in the study area. From this, I suspect that she was a widowed adult female who still held a territory and advertised it but had no partner to do so in a duet. The social status of Ximena is unclear, since all her songs were given from the margin of the study area and had low signal to noise ratios. It was therefore not possible to hear whether the detected great calls were part of a duet song or a solo song.

Calliope disappeared from the study area after April 2017 and was not detected until the end of the study period. In May, a new individual Inna appeared and occupied Calliope's former territory area until August 2017. Then Inna was not found anymore in September 2017 but Filippa, a neighbouring individual, seemed to have shifted her territory to the west and took over part of Inna's former territory. Jolli also moved further south than she was found in the months before Inna disappeared. These shifts in territory occupation can be seen in Figure 15, Appendix I. In all months, there was a maximum of 14 groups present in hearing distance, and probably only 13 groups in September. On average, 8.4 (range: 3-13) different groups were detected on each survey day.

According to the definition that a female classified as a resident when a) her calls were detected on more than 17 days (>33% of days surveyed) and b) when more than half of her songs were localized within the localization area, there were six resident females in the study area (Table 3). Although Jolli was heard on less than 17 days, her territory was lying entirely inside the study area, surrounded by neighbouring groups on all sides. Therefore, she should be counted as a resident as well, adding up to 7 resident females. Calliope was also detected only on 17 days because she disappeared after the first four months. But she should be counted as a resident for the time before she disappeared and her territory was taken over by the new individual Inna. To sum up, before Inna disappeared from the study area in September, there were a total of 7 groups resident within the localization area of 5 km^2. This leads to a white-handed gibbon density of 1.4 groups/km^2. Filippa, Solfaya, Tepe and Tsubasa were four often heard females whose groups seemed to reside adjacent to the study area. Undulani and Ximena were heard less frequently, their territory seemed to touch the study area only marginally. On average, only 4 (range: 2-5) consecutive survey days were required until all resident groups were detected, and only 2 (range: 1-3) days were required if the rarely singing widow Jolli was ignored.

Table 3: Resident group criteria and status of all 15 identified individuals. Criteria that are fulfilled to qualify as a resident group are in bold.

Individual	Number of days detected	% of localized songs within localization area	Resident status
Calliope	17	**93%**	YES (special case: disappeared)
Filippa	**42**	38%	NO
Gemma	**45**	**84%**	YES
Inna	**23**	**57%**	YES
Jolli	10	**100%**	YES (special case: widowed)
Kokorani	**26**	**59%**	YES
Levina	**46**	**64%**	YES
Nalingi	**34**	11%	NO
Ratu	**36**	**61%**	YES
Solfaya	**47**	29%	NO
Tepe	**18**	8%	NO
Tsubasa	**37**	15%	NO
Undulani	5	17%	NO
Ximena	17	36%	NO
Yuna	**40**	**80%**	YES

Territory analysis

Localization and identification of detected great calls resulted in a data set with 779 data points indicating the mean location of each song (including songs with only 1 great call; Figure 9, left). From these, only the 398 locations lying within the localization area (Figure 9, right) were used to calculate territories as 95% MCP, seen in Figure 10. Due to small sample size, the territories of Undulani and Tepe could not be calculated.
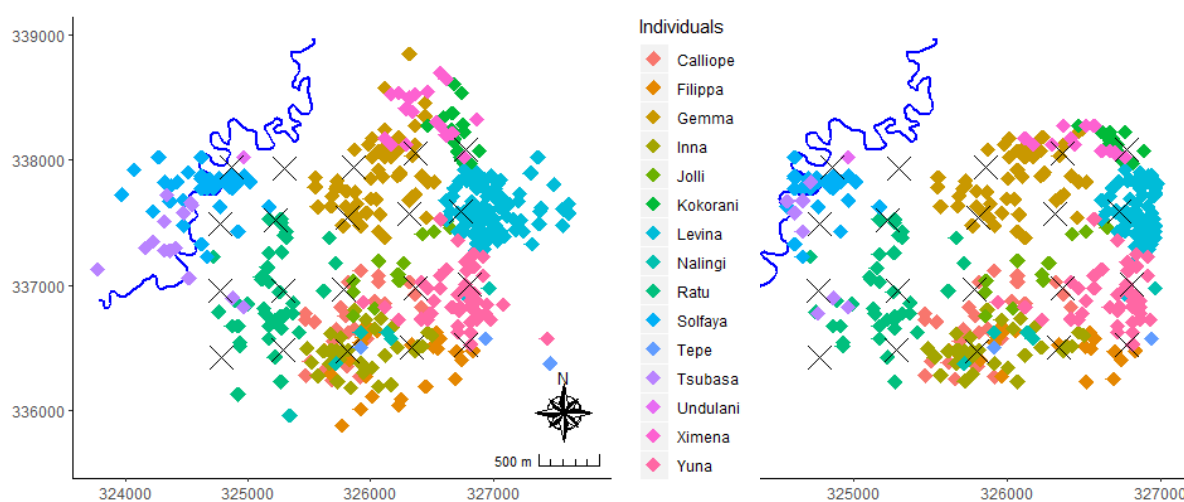
Figure 9: Left: all localized and identified gibbon song locations between January - September 2017. Right: locations of localized and identified songs only within the localization area. This is the data basis used for territory analysis. Blue line: river; X's: locations of recording devices of ALS.
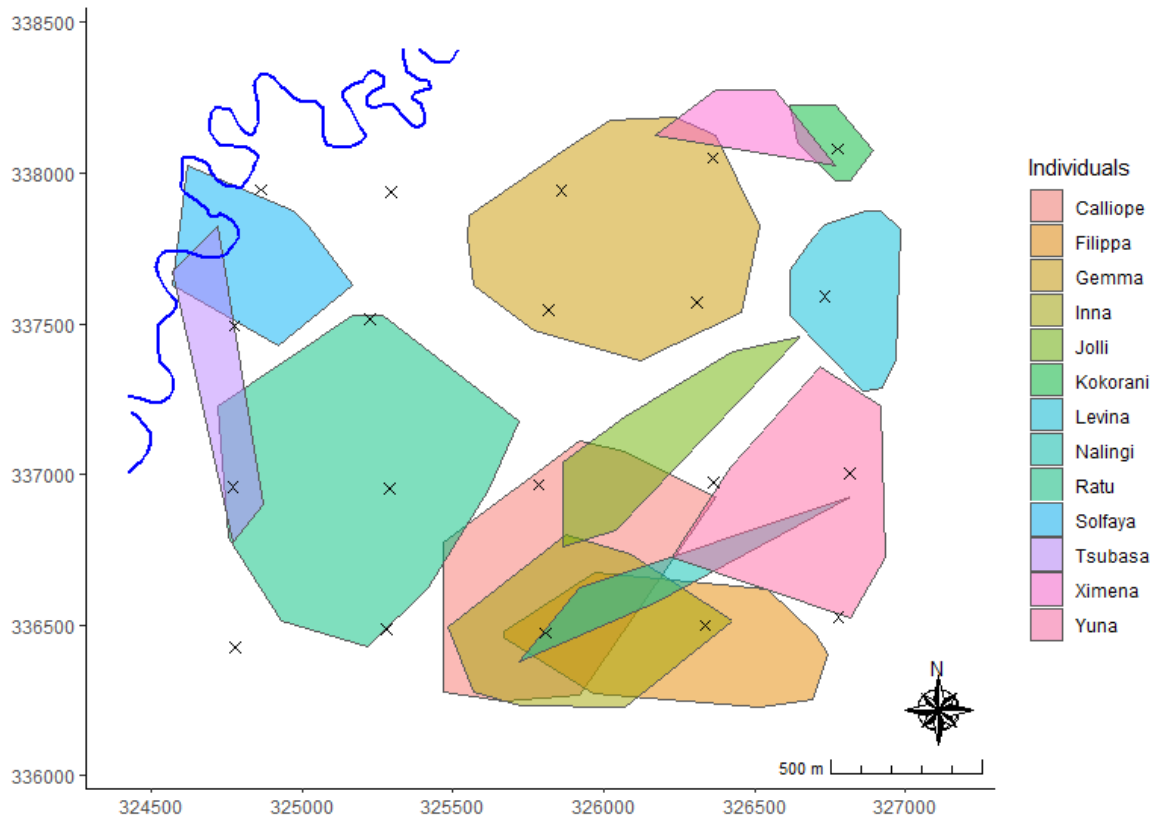
Figure 10: 95% MCP territories of identified gibbon groups. Individuals Tepe and Undulani are missing here, due to limited number of data points for a territory analysis. Blue line: river; X's: locations of recording devices of ALS.

Due to the fact that all localizations lying outside the localization area were ignored for this analysis, it only makes sense to report territory sizes of groups living inside the study area. This was true for the individuals Calliope (light red), Gemma (beige), Jolli (light green), Ratu (green, south west) and Yuna (pink, south east). I am cautious about the groups of Inna, Filippa, Nalingi, Solfaya and Levina, as they all had their territory at the edge of the study area, and it was likely that the extent of their real territory could not be sampled with the recorder grid used. For Inna (olive green), Filippa (orange) and Nalingi (green triangle) in the south, there were many more detections of their calls than the ones that could be localized. In many cases, their calls were recorded only by one or two recorders and did not allow localization. There were many localizations for Levina (light blue, east), Ximena (magenta, north east), Solfaya (dark blue, north west) and Tsubasa (purple, west) that lay outside the localization grid (Figure 9). Although according to the criteria, Kokorani (dark green, north east) was classified as a resident, her territory was too marginal for the calculated territory size to be accurate.

The average territory size for white-handed gibbons in Suaq Balimbing, based on the five central groups (Table 4), resulted in 0.47 km^2 (SD ±0.21). Under the assumption that a gibbon territory covers approximately 75% of a home range (Leighton, 1987), an average gibbon home range in Suaq Balimbing measured 0.63 km^2. Jolli, the widowed individual, had a much smaller territory than the four mated individuals, between half and a quarter of the territory size of the mated females.

Table 4: Territory sizes of groups located inside the study area (left) and groups that have their territory at the border of the study area (right).

Central groups	Territory size (km^2)	Marginal groups	Territory size (km^2)
Calliope	0.50	Filippa	0.35
Gemma	0.56	Inna	0.35
Jolli	0.18	Kokorani	0.04
Ratu	0.72	Levina	0.16
Yuna	0.35	Nalingi	0.10
		Solfaya	0.21
		Tsubasa	0.14
		Ximena	0.08

For three out of the five central groups, the cumulative territory size reached an asymptote with data from about 32 survey days (Figure 11). The territory sizes of Jolli and Yuna increased suddenly at the end of the study period, which falls together with the period when Inna disappeared and Jolli and Yuna set foot closer to Inna's former territory area (Figure 15, Appendix I).
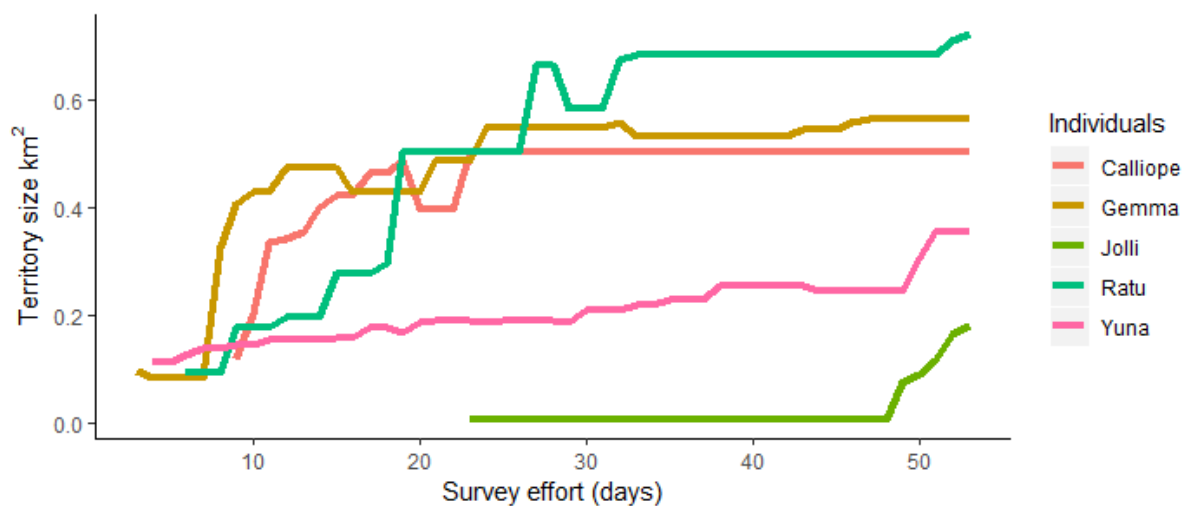
Figure 11: Cumulative territory size, showing how the computed territory size increased with increasing number of survey days. For Jolli, only very few calls were detected and only after 23 survey days, enough data points were available to compute a territory size.

3.3 Influence of territory intrusion pressure and fruit availability on singing intensity

Analyses on day level

On average, the gibbons in Suaq Balimbing produced 5.25 (SD ±2.11) songs per day, 1.32 (SD ±0.62) songs daily per individual. Songs lasted on average 852.8 (SD ±580.8) seconds or 14.3 (SD ±9.7) minutes and great calls were given at a rate of 0.37 (SD ±0.1) great calls per minute. The analysis on day level showed no effect of fruit availability on the total number of songs produced, the best fitting model contained only the number of singing groups (Table 5). However, fruit availability had a significant positive effect on the mean great call rate (z=2.3, p=0.03), increasing it by 0.01 great calls/min (SE

24

±0.004). But it is hard to believe that such a small change is of importance for the calling behaviour of gibbons. The maximum change in fruit availability at Suaq Balimbing in 2017 was 8.5%. This would lead to a maximum increase of the call rate by 0.085 great calls per minute. The mean song duration could not be explained by fruit availability nor the number of singing groups, the null model was the best fitting model.

Table 5: Results of best fitting models on day level to predict the number of songs, mean song duration and mean great call rate. N = 51 days.

	fruit availability			number of singing groups		
Response variable	SE	z value	p value	SE	z value	p value
number of songs	-	-	-	0.03721	6.032	1.62e-09
mean song duration	-	-	-	-	-	-
mean great call rate	0.004433	2.301	0.0256	-	-	-

Analyses on individual level

Significant differences between individuals were shown for the number of songs (Kruskal-Wallis, χ^2= 29.56, p= 0.005), mean song duration (ANOVA, F=2.41, p=0.005) and mean great call rate (ANOVA, F=7.62, p=4.1e-12). However, the duration of songs produced by different individuals was close to the average for all individuals except for Tsubasa (Figure 12). When Tsubasa was excluded from the analysis, song duration did not differ anymore between individuals (ANOVA, F=1.56, p=0.11). Therefore, the results of the song duration model below should be regarded with caution.
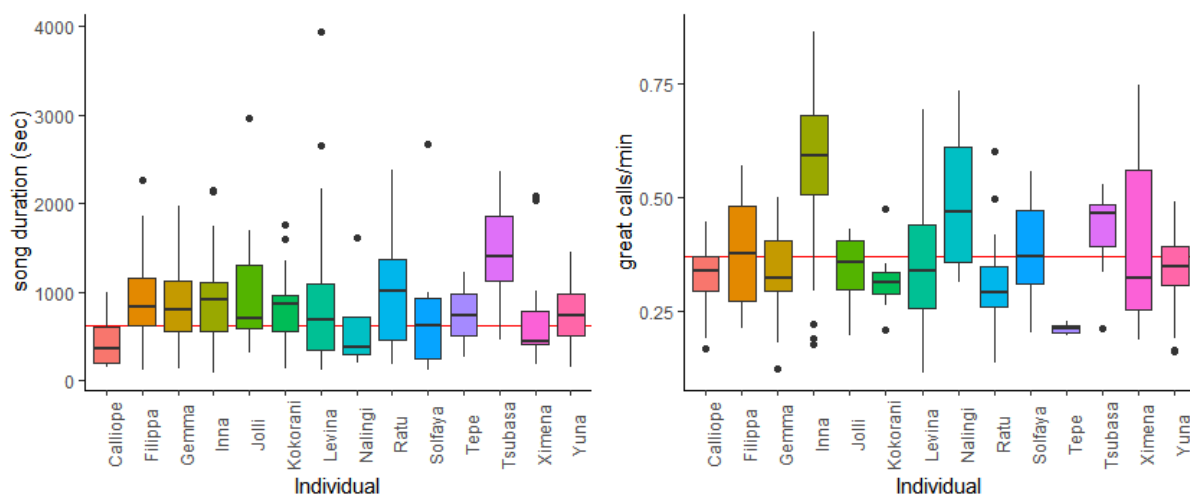

Figure 12: Left: song duration of different individuals. Right: great call rate of different individuals. Boxplots show the median (black horizontal line) and the interquartile range (within boxes). Whiskers extend to the values laying at most 1.5 times from the upper and lower quartiles. Points beyond this range are outliers (black dots). Red line: overall mean song duration and great call rate, respectively. Undulani is missing from this analysis because there was only one song of hers detected.

When comparing the great call rates of different individuals (Figure 12, right), Inna – the individual who took over Calliope's territory after she disappeared – stands out with very high great call rates. When inspecting the great call rates of Inna, Calliope and their neighbours by month (Figure 13), one can see that in the period from May to August, when Inna presumably had to establish herself in her new territory, the great call rates of the neighbouring females tend to be higher than before. This is especially distinct in Filippa's great call rates. Since Filippa is a direct neighbour of Inna and occupies the very southern part of the study area as well, it intuitively makes sense that her calling behaviour is affected the most. I suspect that such changes in territory occupation and the need for a group to

establish themselves in a new territory will affect their calling behaviour, as well as the calling behaviour of direct neighbours. However, this hypothesis was not further tested statistically in the scope of this study.
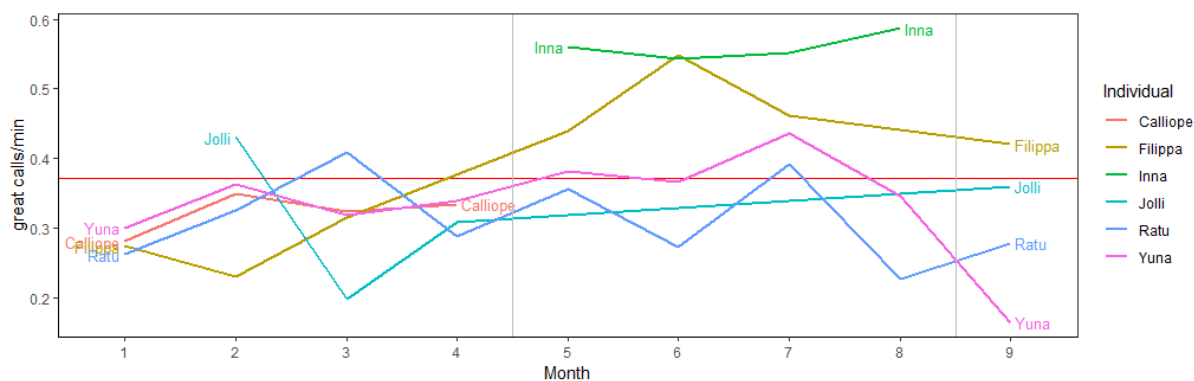

Figure 13: Great call rate per month for Calliope, who disappeared from the study area and Inna, who then occupied Calliope's former territory, and their neighbours. Only songs within the localization area are considered. Red line: average great call rate of all individuals in the study area over the entire study period. Grey vertical lines: approximate times when Calliope and Inna disappeared from the study area.

The model with the lowest AIC value to predict the number of songs given on a day by different individuals contained as fixed variables the number of neighbours and the distance to the song the individual responded to. However, neither of the variables was significant (Table 6).

Table 6: Model output of best fitting model for the number of songs given by an individual on a day. N = 209.

Fixed variable	Estimate	SE	z value	p value
Number of neighbours	0.0494656	0.4056527	0.122	0.903
Distance to responded song	-0.0005434	0.0019942	-0.272	0.785

For mean song duration, the best fitting model contained fruit availability, number of neighbours and the distance to the song the individual responded to. The number of neighbours had a significant positive effect on mean song duration (z=2.442, p=0.0425), increasing it by 419.865 seconds (SE ±171.903) or 7.0 minutes (Table 7).

Table 7: Model output of best fitting model for mean song duration. Significant fixed variable in bold. N = 209.

Fixed variable	Estimate	SE	z value	p value
fruit availability	36.083	49.578	0.728	0.488
number of neighbours	**419.865**	**171.903**	**2.442**	**0.0425**
distance to responded song	1.012	0.926	1.093	0.3042

The mean great call rate was best fitted by the null model, meaning that none of the defined fixed variables were able to predict the mean great call rate.

4. Discussion

This study investigated and confirmed the suitability of an acoustic location system (ALS) as a tool for frequently used analyses in wildlife monitoring and conservation, namely group density estimation and territory analysis on the example of white-handed gibbons in a peat swamp rainforest in Sumatra. Gibbon calls recorded with the ALS could successfully be localized and the calling individuals were identified with a manual identification method based on call source locations and idiosyncrasies in the structure of female great calls. This allowed the assessment of gibbon group density and territory sizes. It was also possible to collect quantitative data on vocal and ranging behaviour. Simple statistical tests were carried out to relate these behaviours to territory intrusion pressure and environmental factors (fruit availability), but there is potential for additional hypotheses to be tested with the data.

4.1 Group density, territories and behaviour of gibbons in Suaq Balimbing

Group density

At our study site Suaq Balimbing, the density of white-handed gibbon groups was 1.4 groups/km^2. This is within the range of group densities found in peninsular Malaysia (Kuala Lompat: 0.7 groups/km^2, Gittins & Raemaekers, 1980; Tanjong Triang: 2 groups/km^2, Ellefson, 1968) and Borneo (2.6 groups/km^2 for Bornean agile gibbons, Cheyne et al., 2008). The group density of the population in Khao Yai, Thailand, lays on the upper end of the spectrum with 6.5 groups/km^2 (Chivers, 1984).

Gibbon territories and spatial distribution

The comparably low group density in Suaq was coupled with a large home range size. The average territory size was 0.47 km^2, resulting in an average home range size of 0.63 km^2 assuming that gibbon territories covered 75% of a home range (Leighton, 1987). This is larger than any of the home ranges reported in the literature for *Hylobates lar*. Gibbon home ranges measured 0.20-0.58 km^2 in peninsular Malaysia (Gittins & Raemaekers, 1980; Whitten, 1984), 0.53 km^2 in Borneo (Cheyne et al., 2008) and approximately 0.24 km^2 in Thailand (Reichard & Sommer, 1997; Bartlett et al., 2016). A study on orangutans revealed that the home ranges of orangutans in Suaq Balimbing were significantly larger than home ranges of any other orangutan population recorded (Singleton & van Schaik, 2001). They proposed that the low food plant species richness in swamp forests drives the orangutans to maintain a larger home range in order to uphold an adequate diet. This may apply to the gibbons of Suaq as well. On top of that, fruit availability is relatively stable year round in Suaq Balimbing. This was also true for 2017, when the fruit availability index ranged between 8% and 16%. The constant supply of high energy food sources without periods of food scarcity might enable the gibbons to maintain and defend a larger territory than in forests where there are periods of fruit scarcity, such as for example in Khao Yai, Thailand (FAI: <1% - 12%, Bartlett, 2009), and Sabangau, Borneo (FAI: <1% - 8%, Cheyne, 2010).

The territories were more spread out in the western half of the study area, where only 4 out of 15 identified groups were found (Figure 10). The remaining 11 groups were concentrated in the eastern half of the study area, especially in the southeast, where 7 groups were found. Possible explanations for this distribution of gibbon groups may be habitat characteristics and the presence of sympatric gibbon species. Hamard (2010) found that canopy cover and tree height are strongly correlated with gibbon density. In the northwest, the study area is bordering on the Lembang river, which comes with a transition to a different plant species composition (more spiny, palm-like plants, fewer large fruit trees) and more open canopy as well as higher swampiness compared to the rest of the study area. In contrast, on the southern end, the forest floor is dryer than the rest of the study area, potentially

supporting higher trees and higher canopy coverage. There is, however, no systematically collected data available on differences of these habitat characteristics within the study area to test this hypothesis. On the other hand, siamangs, another member of the family Hylobatidae, are known to occur sympatrically with lar gibbons (Grether, Palombit, & Rodman, 1992). Siamangs were heard regularly in Suaq Balimbing and their calls were also present in the sound recordings. An assessment of siamang locations and territories using ALS could reveal whether they affect the spatial distribution of lar gibbons in Suaq Balimbing.

The territory analysis using ALS over a period of several months also revealed anecdotal but not less interesting events of changing territory ownership. Calliope, a mated female occupying a territory in the southern part of the study area, disappeared after the first four months analyzed. In her place, a new individual Inna entered the study area and occupied Calliope's former territory for at least four months. It seems that after that, Inna also disappeared from the study area and shifts of the territory boundaries could be observed for two neighbouring groups. This is the kind of data that could only be collected with regular focal follows of habituated gibbon groups. It would be difficult to obtain such data in the same extent with other monitoring methods such as camera trapping or even with regular surveys with human listening posts. Even with focal follows of habituated groups, it would require several follow teams to cover the extent of the study area in order to get a holistic view on what is happening in the entire study area. But now we may ask, what happened to Calliope? It can be speculated about different explanations. First, Calliope might have died a natural death. Terleph et al. (2016) found that call features such as the frequency range of climax notes, maximum F0 frequency and the "duty cycle" of a climax decreased with age. Thus, a further investigation might reveal whether Calliope was an old individual who might have died a natural death. Second, Calliope might not have died but been evicted by Inna. Although gibbons have very stable home ranges over the course of many years (Bartlett et al., 2016), several changes of adult group compositions as well as territory take overs by males as well as by females have been observed (Brockelman et al., 1998). Certainly, there are more explanations possible, such as predation or the effects of human disturbances.

Gibbon calling behaviour related to territorial intrusion pressure and fruit availability
Fruit availability was shown to have a significant positive effect on the overall mean great call rate given by all individuals. However, this effect was so small that it is questionable whether it is of any importance for the gibbons. Fruit availability had no effect on the total number of songs produced, nor on the mean song duration. On the level of individuals, no effect of fruit availability was shown on gibbon singing behaviour either. This complies with the findings of Cheyne (2008), where no significant change was observed in gibbon singing behaviour in periods of low food availability. It should be noted though, that fruit availability did not vary greatly between different months in Suaq Balimbing, so there may have been no need for the gibbons to change their singing behaviour, as food and therefore energy was never in short supply.

Only one of the defined variables reflecting a measure of territorial intrusion pressure, namely the daily number of neighbours (defined as the number of groups singing within 1000 m distance of the focal individual on a given day), was found to have a significant positive effect on the mean song duration. None of the other variables (distance to songs in hearing distance and to songs the individuals responded to) had an influence on the number of songs an individual produced, the mean song duration and the mean great call rate.

Although no significant relationships were found between most of the variables tested, it was possible to derive quantitative data on gibbon calling and ranging behaviour using the ALS. There is potential for more in-depth analyses to be carried out using the obtained data, for example by defining measures

that may better reflect the territory intrusion pressure than the ones investigated in this study. The great call rates of several individuals showed distinct differences between the time period before the new female Inna settled in the study area and the months thereafter. The correlation between the novelty of an individual's territory and the calling behaviour of the new individual and its neighbours would be another interesting question to look into.

4.2 ALS as a tool for gibbon passive acoustic monitoring

ALS proved a suitable method for the monitoring of wild, unhabituated gibbon groups. This is a great chance for conservation and monitoring activities, especially in habitats such as the peat swamp rainforest in Suaq Balimbing, where field conditions make data collection via focal follows cumbersome for researchers.

A main advantage of ALS is the possibility to simultaneously monitor all the gibbon groups in the study area. In the same amount of survey time, more data could be collected on gibbon calls than studies using point count approaches with human listening posts or focal follows. During the 53 days analyzed, 3352 great call events were detected which belonged to a total of 465 song bouts given by the identified individuals. This is an average of 8.8 song bouts detected per survey day. Compared to studies relying on human listeners, this is double the output. Cheyne (2008) recorded 210 song bouts from 12 groups of Bornean agile gibbons (*Hylobates albibarbis*) within 50 survey days (in a survey area covering 4.62 km^2), while Chivers and Raemaekers (1980) recorded 1139 call bouts during 269 days of field observations over the course of 10 years. This results in an average of 4.2 recorded song bouts per survey day, half the output of the ALS used in Suaq Balimbing. This is likely due to the larger detection area covered by this ALS with 20 recording units in comparison to the studies using fewer simultaneous listening posts. A direct comparison study, however, would confirm whether the increased call detection in Suaq can be fully accredited to the monitoring method using ALS or whether there are true differences in the call production rate between the studied populations. In this study, an average of 8.4 (range: 3-13) different females were detected on each survey day and 4 (range: 2-5) survey days were required to detect all resident females. This is similar to the 5 days reported by Cheyne et al. (2008) until all groups were heard.

Recording the gibbon calls with 20 time-synchronized recording units also allowed an accurate localization of the callers, with mean localization errors of only 52.2m (SD ±54.7m) for a localization area extending 200 m outside the recorder grid. Thus, it was possible to assess the spatial distribution of calling gibbon groups within an area of 5 km^2. This addresses one of the concerns raised by Rawson (2010), where he criticized the uncertainties of triangulation accuracies in conventional gibbon surveys with human listening posts. ALS, as opposed to these conventional methods, is not prone to localization inaccuracies due to subjectivity and based on the experience of researchers. What is important, however, is to assure correct time-synchronization between the individual recording units, as all errors in the time difference of arrival (TDOA) of the acoustic signal can lead to errors in the triangulations.

Another aspect that Rawson (2010) criticized in traditional point count methods is the somewhat arbitrary convention that calls heard 500 m or more apart from each other are considered to belong to different groups of gibbons. This is problematic if the territory of the studied gibbons does not conform to the assumed circular territory of approximately 0.20 km^2 in size. Using the calls recorded by the ALS, I was able to distinguish individuals through a combination of spatial information and idiosyncrasies in female great call structures. 86% of all detected great calls could be assigned to one of the 15 identified individuals. If solely the spatial information would have been used, it is likely that

some of the individuals found at the margin of the study area would not have been recognized as separate individuals. Some individuals that have been detected on different days at locations more than 500 m apart, for example Ratu, would have been falsely classified as different individuals, while calls from different individuals detected at similar locations would have been pooled together as one individual. In the latter case, the changes in territory ownership observed in the southern part of the study area would not have been discovered. In a broader context, the combined method for caller identification is less likely to over- or underestimate group densities. The gain in identification accuracy, however, needs to be weighted up against the additional initial time investment to distinguish and describe different individuals in the study area. For continuous or repeated surveys in the same area, it is certainly an investment worth making as previously identified individuals can be recognized and changes in territory ownerships become visible. If the aim is, however, a quick one-time assessment of gibbon group densities in a large survey area, researchers might prefer a less time intensive method and accept higher chances of under- or overestimating group densities. With further research, it may be possible to develop a reliable unsupervised identification algorithm for gibbons and also other species of interest.

Not only the increased output on recorded song bouts and increased accuracy of localizations and individual identification, but also the fact that the monitoring effort of gibbon calling activity covers the entire extent of the study area at all times speaks in favour of the ALS. This opens opportunities to investigate interactive and competitive calling behaviours between gibbon groups. Furthermore, the collection of additional acoustic data comes with practically no additional effort. A ten days long survey does not require a higher effort than a five days long one, let aside the analysis of the additional data recorded. Therefore, I conclude that it is a good tool in semi-long-term studies of several weeks or months.

4.3 Limitations and challenges of automated PAM and ALS

With so many advantages over conventional methods in gibbon studies, what are the limitations of automated PAM and ALS to consider?

First of all, PAM is naturally restricted to the study of acoustically conspicuous species and individuals. In the case of the gibbons in Suaq Balimbing, it was only possible to assess the density of territory holding groups but not population density, because juveniles and individuals without a home range do not produce the great calls this study focused on. Therefore, group sizes and the number of rovers was unknown. It is also only possible to obtain data that is in some way related to the production of the vocalizations of interest. Studies for example on feeding ecology or social interactions of the subjects will still require field observations.

For long-term studies with ALS, researchers will be challenged by the question how to store such a large amount of data. The sound recordings made with the ALS in Suaq Balimbing during one year resulted in more than 20 TB of audio data. Despite technological progress making storage devices with high capacities more and more affordable, it can still be costly to store and back up data of this volume.

Processing the collected acoustic data is not less challenging. The use of a machine learning approach for the detection of acoustic events of interest was shown to be a real advantage in terms of time efficiency over manual scanning and labeling. Automated PAM studies on a variety of animal species developed and successfully applied detection and classification algorithms (e.g. Ganchev & Potamitis, 2007; Ganchev et al., 2015; Kalan et al., 2015). However, there are no universal software packages that can be used to detect and classify sounds of a wide range of species from different study areas. Most

studies developed their own algorithms tailored to their purpose. In order to make PAM more accessible to biologists and conservationists with limited programming skills, it would be highly desirable to develop a common framework facilitating organized storage and access of acoustic data, development of detectors and classifiers and use of existing algorithms as well as providing tools to visualize and analyze the acoustic data - similar to what was offered by the acoustic platform used in this study.

5. Conclusion

This study showed that with ALS, it was possible to assess group densities and home ranges of white-handed gibbons, and to collect quantitative data related to their vocal and ranging behaviour. The methods applied in this study can be adopted for future studies on other vocally conspicuous and territorial species such as other gibbon species and birds. In this case, the size and set up of the recorder grid would need to be adjusted to the vocal and behavioural characteristics of the study species and a species-specific detection algorithm may need to be developed. Although the initial time investment for the development of a tailored detection algorithm as well as the identification of individuals is relatively high, ALS is an objective and reliable method for population density and territory assessments, allowing the collection of data over a variety of spatial and temporal extents. It appears also suitable for the comparison of findings between study sites, different habitat types or to monitor changes over time.

On the analysis side, the development of a common framework for the processing and analysis of acoustic data would be desirable in order to make ALS and PAM more applicable for conservationists and ecologists with limited programming skills. This would benefit various applications in the context of wildlife and habitat conservation. As PAM is not limited to the collection of data on one target species at a time, all vocal species in a study area can potentially be monitored. Therefore, PAM can be used for general biodiversity assessments and ecosystem health studies relying on the analysis of a habitat's soundscape. It can also be used to monitor human activities, such as illegal logging activities in protected habitats. Such observations allow conservationists to target conservation efforts in the areas of most concern.

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Title picture: Caroline Schuppli, 2013, The Suaq Project

Figure 1: IUCN (International Union for Conservation of Nature) 2008. Hylobates lar. The IUCN Red List of Threatened Species. https://www.iucnredlist.org/species/10548/3199623 [accessed: December 2017]

Figure 3 left: Google Maps, URL https://www.google.com/maps [accessed: December 2017]

Figure 3 right: Chigusa Keller, 2016

Figure 14: Urs Wipfli, 2017

Appendix I

Figure 14: A recording unit of the ALS set up in Suaq Balimbing. On top (black) is the GPS device for time-synchronization, a metal cover shields the recorder from rain and falling debris. The recorder (Song Meter SM3, Wildlife Acoustics Inc.) is connected via cable to a SMX-II microphone deployed in 10 m height in the canopy and is powered by a 12 V, 18 Ah dry gel battery (inside yellow case). The battery was charged by a 50 W solar panel. (Photo credit: Urs Wipfli, 2017)

Table 8: Validation results of the great call detection algorithm. Detections by the algorithm were compared to manually labeled data from 22 hours (427.05 recording hours by 20 recorders). GC: great call, tp: true positive, fp: false positive, fn: false negative.

	Validation set 1	Validation set 2	Summary
Date/time analyzed	24.01.2017 05:00-19:00	25.01.2017 05:00-13:00	
Day hours/recording hours	14h/271.05h	8h/156h	22h/427.05h
Manual GC detections	269	544	813
# total detections	521	349	870
# GC events	78	109	187
# songs	16	21	37
# tp detections	139 (26.7%)	336 (96.3%)	475 (54.6%)
# fp detections	382 (73.3%)	13 (3.7%)	395 (45.4%)
# fn detections	130 (48.3%)	208 (38.2%)	338 (41.6%)
# call events detected	57/78 (73.1%)	98/109 (90.0%)	155/187 (82.9%)
# songs detected	15/16 (93.8%)	19/21 (90.4%)	34/37 (91.9%)
Comment	All missed call events outside grid	All missed call events outside grid	
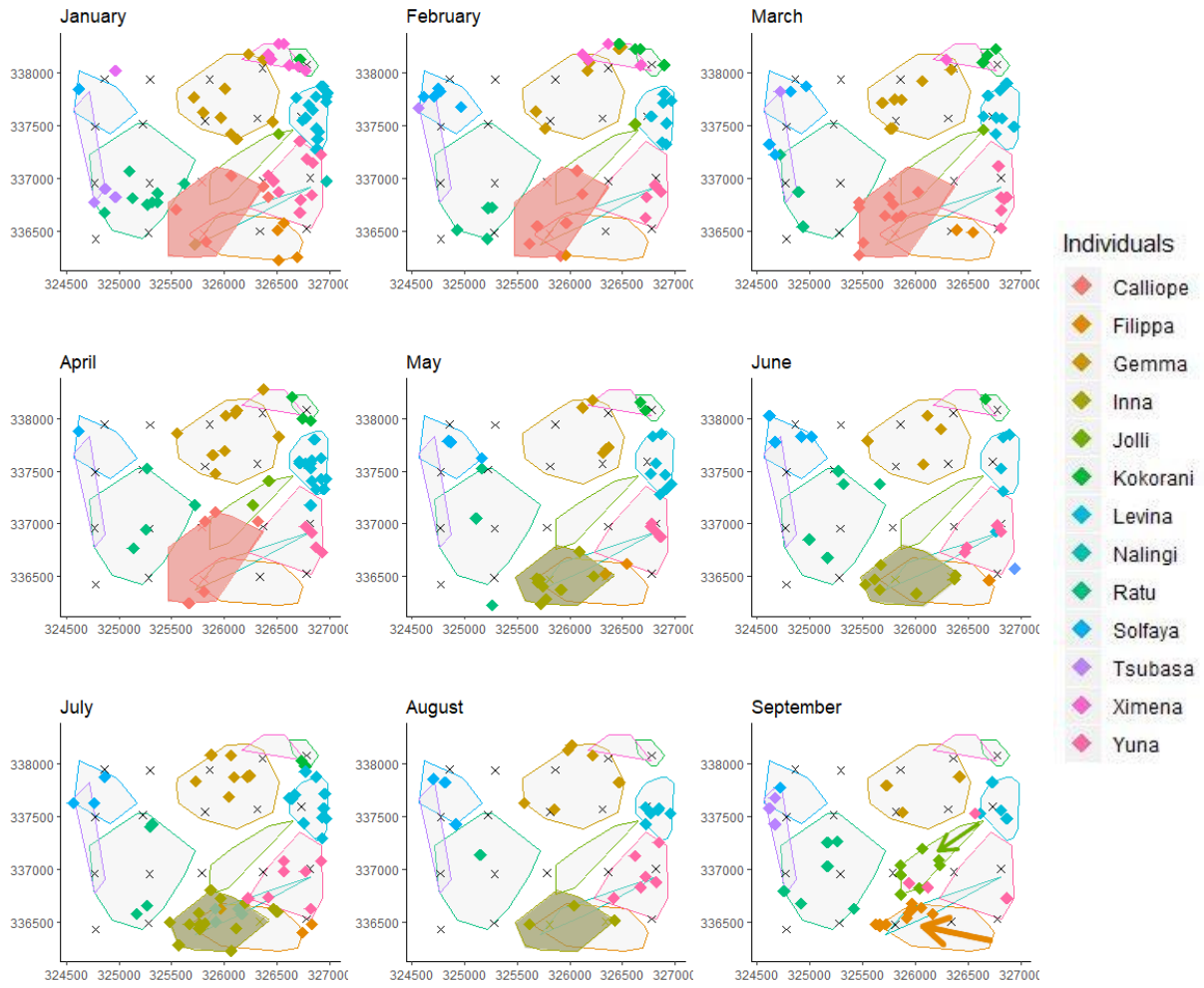
Figure 15: Polygon outlines: territories of the gibbon groups in Suaq Balimbing. Highlighted in red: Calliope; olive green: Inna. Points show locations of songs given in each month, making visible the shifts in the territory occupation for the groups in the south of the study area. Orange arrow: Filippa; light green arrow: Jolli.

Appendix II

Identification catalogue of the 15 individuals found within hearing distance from the study area in Suaq Balimbing. Although the number of notes could differ between calls of the same individual, general characteristics of the great call structure showed constant similarities within and across days and could be distinguished from other individuals. Orange squares indicate the second note and the climax note of the call. All spectrograms are displayed here within the frequency range of 500 – 1500 Hz.

Calliope
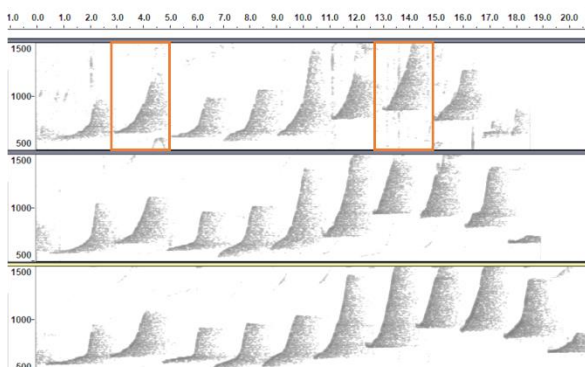
09.02.2017   10.02.2017 / 22.03.2017 / 06.04.2017
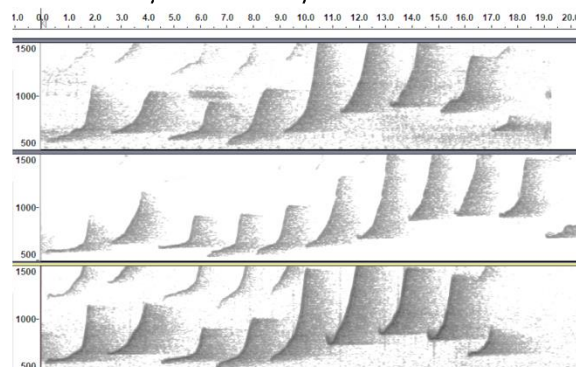
Social status: mated adult female
Number of notes: many notes, between 8-11
General GC shape: relatively flat.
2nd note: starts low at about 650 Hz
Climax note: lowest point ca. 900-950 Hz
Other comments: Notes look fairly uniform throughout the call

Filippa
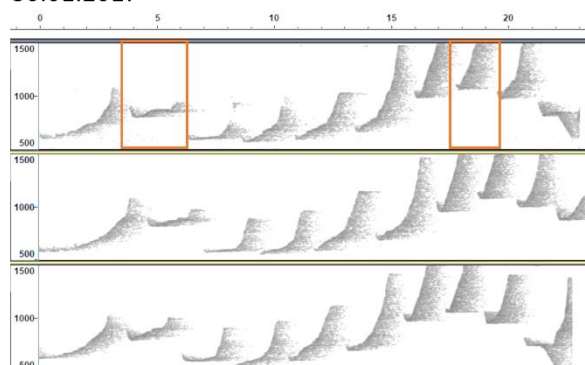
30.01.2017   31.01.2017 / 05.04.2017 / 20.07.2017
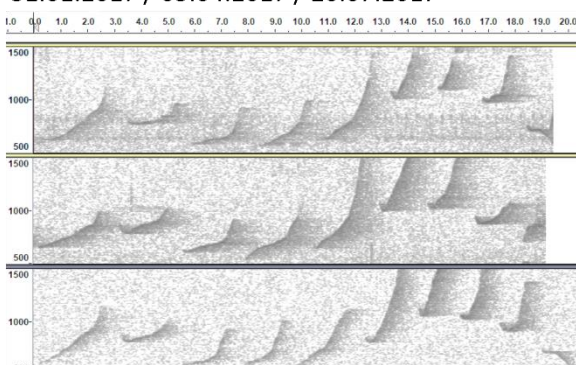
Social status: mated adult female
Number of notes: many notes, between 9-11
General GC shape: wavy
2nd note: strongly leaning forward, starting with a hook and often in a wavy shape.
                               Lowest point of hook ca. 800 Hz.
Climax note: lowest point ca. 1000 Hz

Gemma

25.01.2017
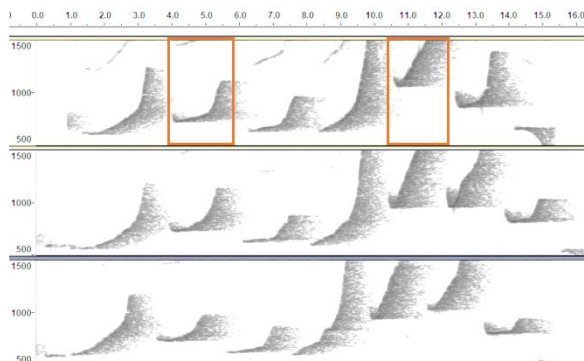
24.01.2017 / 27.01.2017 / 19.07.2017
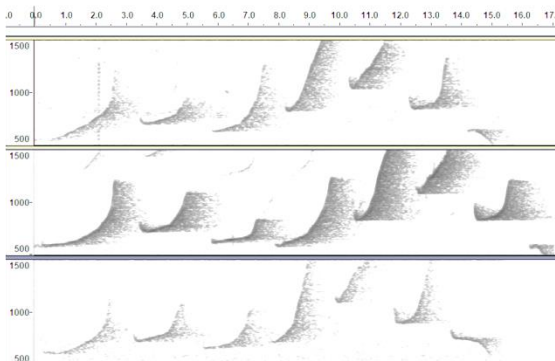
Social status:	mated adult female
Number of notes:	few notes, between 6-8
General GC shape:	wavy
2nd note:	starting with a hook, nearly horizontal before rising steeply. Lowest point ca. 700 Hz
Climax note:	lowest point ca. 1000 Hz

Inna

27.05.2017
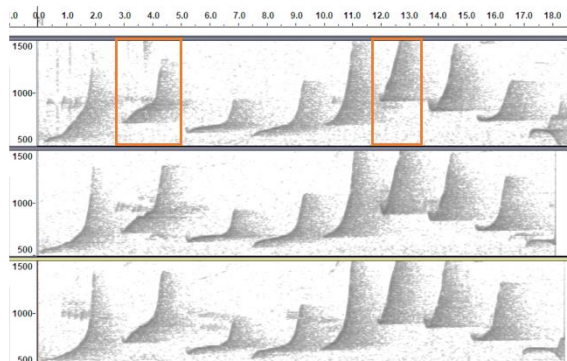
28.05.2017 / 07.06.2017 / 13.07.2017
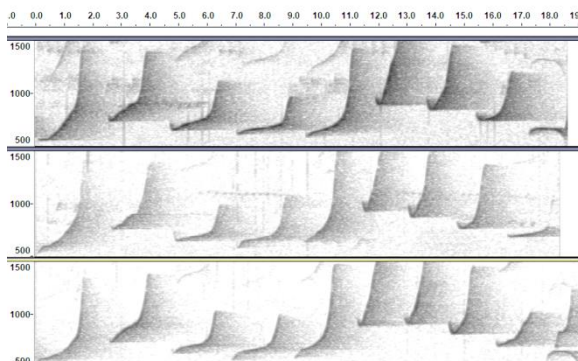
Social status:	mated adult female
Number of notes:	very stable number of notes, usually 9
General GC shape:	Constant drop of note starting point after climax note. Climax and following 2-3 notes with hook.
2nd note:	starting with a steady rise, then sudden and nearly vertical rise, creating an angle. Lowest point ca. 700 Hz.
Climax note:	lowest point ca. 900 Hz
Other comments:	very stable call structure and note shapes across days.

Jolli
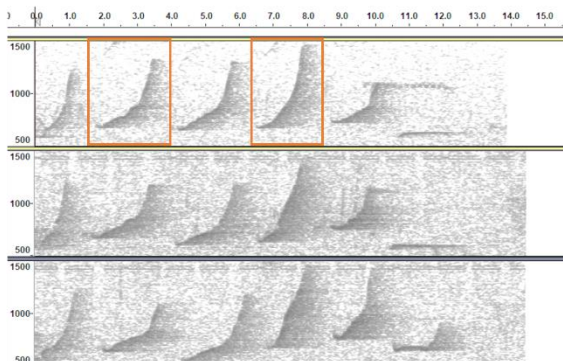
13.02.2017   **25.03.2017 / 02.04.2017 / 11.09.2017**
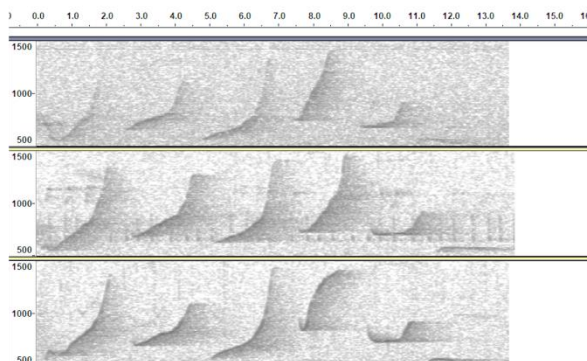
Social status:	not mated, probably widowed
Number of notes:	few, 6-7
General GC shape:	not particularly wavy
2nd note:	relatively long, leaning forward and with an angle
Climax note:	lowest point ca. 650 Hz
Other comments:	

Kokorani
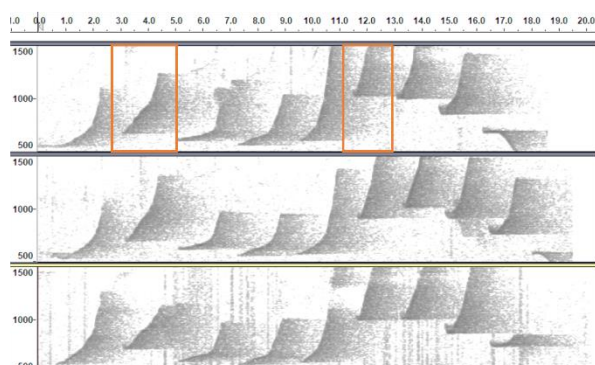
25.01.2017   **26.01.2017 / 10.02.2017 / 07.06.2017**
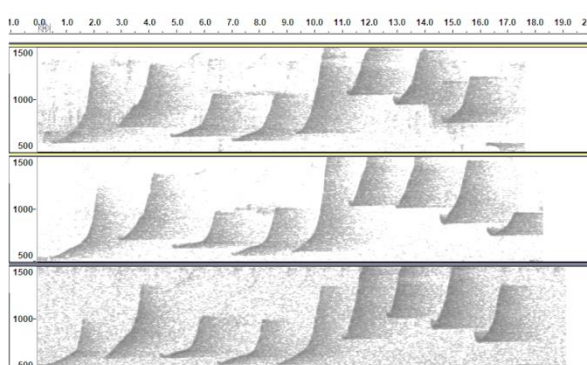
Social status:	mated adult female
Number of notes:	ca. 9
General GC shape:	constant drop in note starting point after climax
2nd note:	steep nearly vertical rise
Climax note:	lowest point ca. 1000-1050 Hz, with hook
Other comments:	

Levina
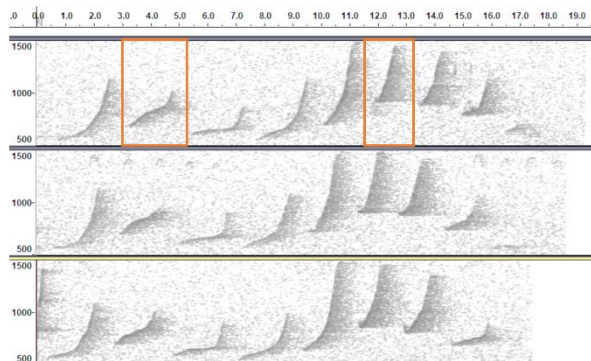
27.01.2017   28.01.2017 / 31.01.2017 / 03.04.2017
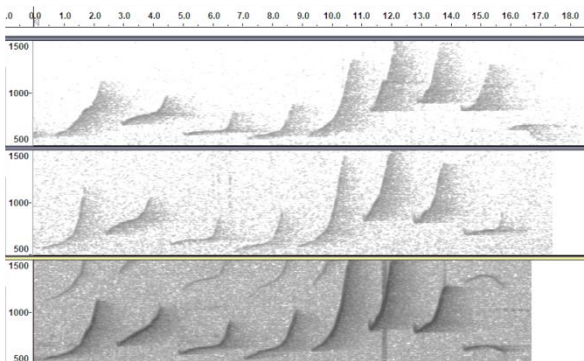
Social status: mated adult female
Number of notes: ca. 8-9
General GC shape: climax note and following notes with small hooks
2nd note: leaning forward, often with a little hump before the vertical rise
Climax note: lowest point ca. 850 Hz, with hook
Other comments:

Nalingi
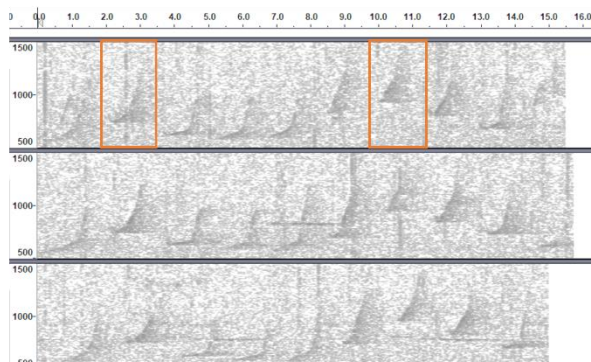
24.01.2017   26.01.2017 / 29.05.2017 / 13.07.2017

Social status: mated adult female
Number of notes: 8-10
General GC shape: rather flat,
2nd note: lowest point ca. 750 Hz, with hook
Climax note: lowest point 850-950 Hz, with big hook
Other comments: mostly heard around Recorder 04, but bad quality (far away)

Ratu

25.01.2017
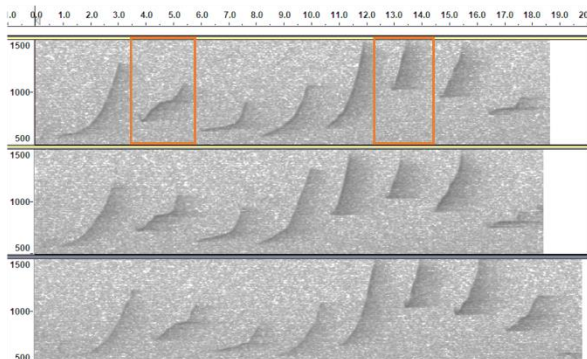
26.01.2017 / 29.01.2017 / 19.07.2017
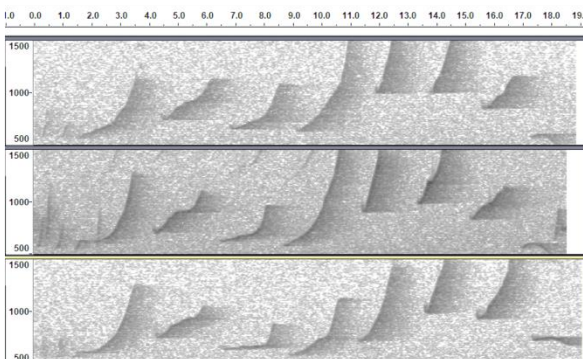
Social status: mated adult female
Number of notes: 8-9
General GC shape: second hump shape pronounced
2nd note: often undulating and leaning forward, lowest point 700-750 Hz
Climax note: lowest point ca. 1000 Hz, with hook
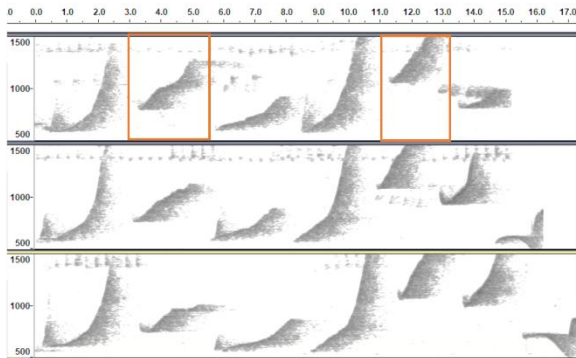Other comments:

Solfaya

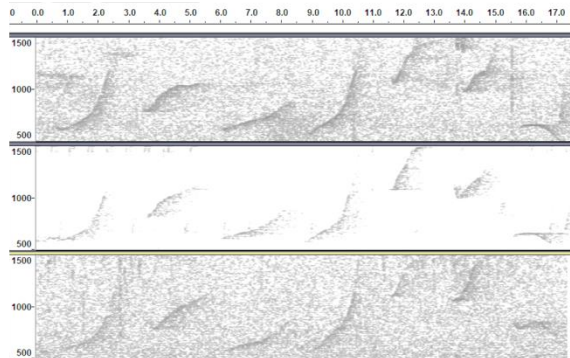**29.01.2017**
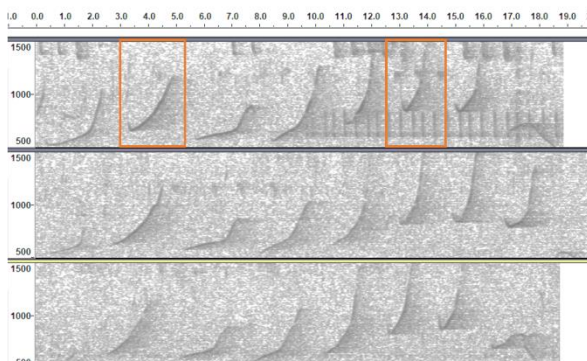
12.02.2017 / 15.04.2017 / 18.07.2017
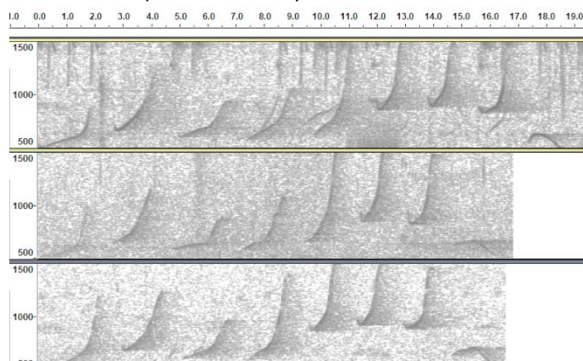
Social status: mated adult female
Number of notes: 7-9
General GC shape: most notes are very steep and with hook
2nd note: lowest point ca. 650 Hz, with hook
Climax note: with hook, often 2-3 notes at same frequency, lowest point ca. 850 Hz
Other comments:

Tepe

23.03.2017   27.01.2017 / 30.01.2017 / 06.04.2017
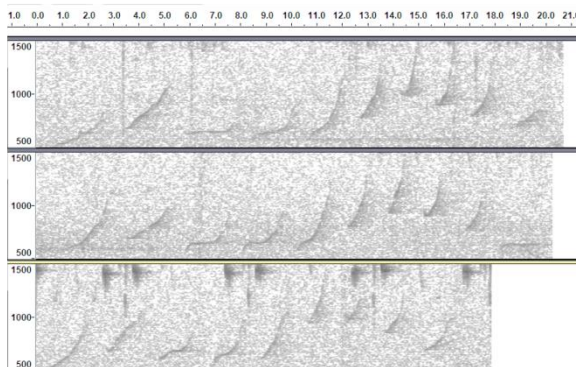

Social status: mated adult female
Number of notes: 5-7
General GC shape: note preceding climax note ranges over many frequencies,
                      then sudden jump up to climax note
2nd note: lowest point ca. 750 Hz, leaning forward, often in a humped shape
Climax note: very high, lowest point ca. 1050 Hz, with hook
Other comments: heard in south east mostly outside of recorder grid. Only few good quality recordings

Tsubasa
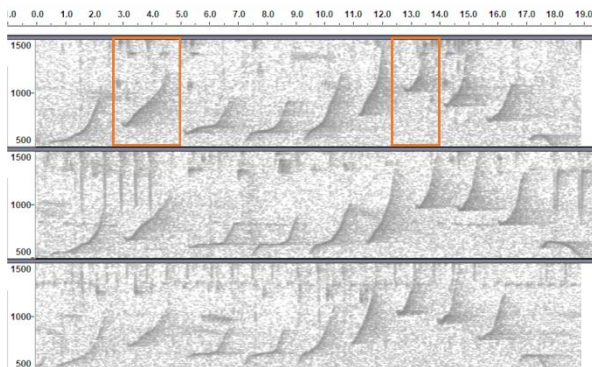
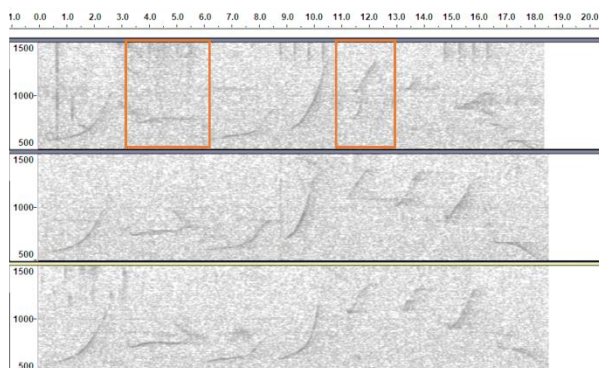13.07.2017   26.01.2017 / 30.01.2017 / 17.07.2017
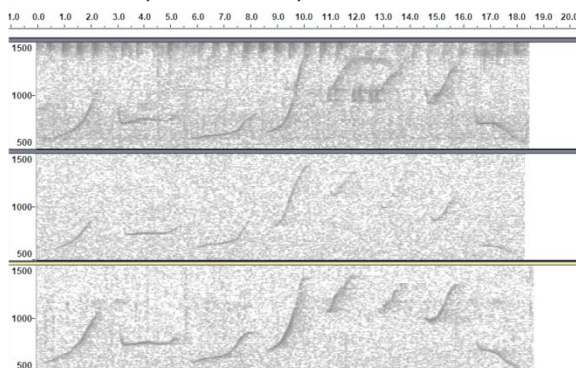

Social status: mated adult female
Number of notes: 10-12
General GC shape: distinct hump around climax note, made of ca. 4 notes
2nd note: lowest point 650-700 Hz, with hook
Climax note: lowest point 950-1050 Hz, with hook
Other comments: 2-3 notes following the first peak note have two bends, like a vertical z-shape

Undulani

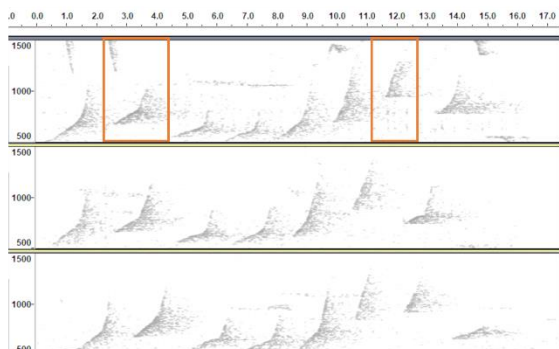**25.01.2017**   **12.02.2017 / 18.07.2017 / 12.08.2017**
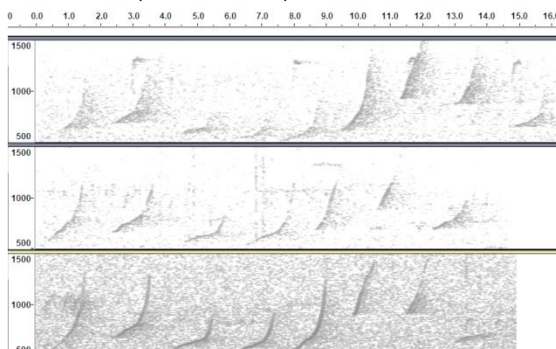

Social status: mated adult female
Number of notes: 8
General GC shape: second hump with relatively flat top shape
2nd note: undulated shape, nearly horizontal, lowest point ca. 750 Hz
Climax note: lowest point ca. 1050 Hz, with hook
Other comments: heard in only few occasions, lives outside study area

Ximena

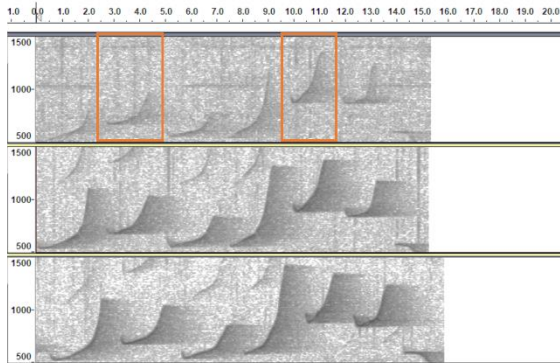**30.01.2017**   **25.01.2017 / 09.02.2017 / 23.03.2017**
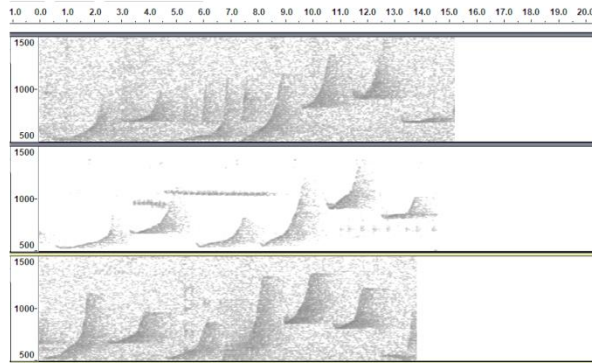

Social status: unknown
Number of notes: 8-9
General GC shape:
2nd note: starting with a steady rise, then sudden rise, creating an angle. Lowest point ca. 650 Hz.
Climax note: lowest point 900-950 Hz
Other comments: most notes look very 'edgy' with this distinct angle

Yuna

24.01.2017   26.01.2017 / 30.01.2017 / 20.07.2017

Social status:	mated adult female
Number of notes:	6-7
General GC shape:	rather short with ca. 15 s
2nd note:	nearly horizontal before rising steeply. Lowest point 650-700 Hz.
Climax note:	lowest point ca. 850-900 Hz, with big hook, often followed by second similar note
Other comments:	

Personal declaration

I hereby declare that the submitted thesis is the result of my own, independent, work. All external sources are explicitly acknowledged in the thesis.

Date   Signature

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