Long calls of flanged male orangutans (*Pongo spp.*) reveal geographic variation in competition behaviour

An approach using an Acoustic Localization System

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Abstract

Intra-sexual competition occurs over factors that limit an individual's reproductive fitness. Primate male's maximum reproductive output is limited by access to fertile females, and the intensity and outcome of male-male competition can vary depending on aspects of female social organization, reproductive synchrony and monopolization potential. Orangutan females are semi-solitary, have non-advertised ovulation and long inter-birth intervals. These factors suggest intense male-male competition over infrequent fertilization opportunities. Geographic variation seen in orangutans implies that populations operate under different mating systems that may be island based. In Sumatra, there seems to be a higher potential for female monopolization, which leads to a clear 'locally dominant male' and stable dominance hierarchies. Whereas in Borneo a 'promiscuous roving male' mating system has been described with more instable dominance hierarchies. A previous study of flanged male orangutan competition in Tuanan, Borneo through the long call mechanism found a 'confrontational assessment' model of male-male competition. Tuanan male ranging was found to be dictated by fruit availability, with long call and response behaviour being adjusted based on presence of fertile females and other males. This study replicates the novel Acoustic Localization System (ALS) method of passive acoustic data collection used in that study in Suaq, Sumatra. A total of 184 days of complete ALS coverage were analyzed for this analysis totaling 2,196 long calls between the two sites. We tested if flanged males compete the same under these different mating systems, by analyzing male presence, daily long call rates, and long call response behaviour. Suaq male ranging behaviour does not appear to be influenced by fruit availability levels and overall there are less males passing through the study site on a yearly and daily basis. There are less daily long calls occurring within the Suaq study area and Suaq males don't display the same distinct pre-dawn calling peak found

in Tuanan males. Long calls are less likely to be responded to in Suaq compared to Tuanan, with a more delayed response latency. Suaq males with heighted spontaneous calling rates do not have heightened long call response rates, which is seen in Tuanan. These results suggest that the 'confrontational assessment' approach of male-male competition found in Tuanan is not found in Suaq, and Suaq flanged males compete through 'systematic exclusion'. Frequent confrontations are not recorded or necessary in Suaq due to more stable dominance hierarchies and less unfamiliar, roving males. This thesis provides evidence for innate geographic variation in flanged male orangutan competition behaviour that goes beyond immediate forest productivity.

1.0 Introduction

1.10 Background

1.11 Sexual Selection

Darwin's Descent of Man (1871), outlined the basis of sexual selection theory, a form of natural selection. Sexual selection can be broken into two components, inter- and intra-sexual selection, where differential reproductive success of animals is not necessarily based on environmental fitness, but competition for access to mates. Secondary sexual characteristics can evolve as a consequence of these sexual selection components. Inter-sexual selective advantage comes from attractiveness to the opposite, choosing sex, with secondary sexual components being costly signals to indicate high genetic quality and vigor. Intra-sexual selection is based on out competiting same-sex individuals for mate access with functional fighting adaptations evolving as secondary sexual characteristics. The most common form of intra-sexual selection is the more intense, male-male competition (Greenwood, 1980).

1.12 Competition

Intra-sexual competition occurs over limiting ecological factors and along with differences in parental investment, dictate different reproductive strategies for males and females to maximize potential reproductive fitness (Trivers, 1972). These limiting factors provide the basis of competition which falls on a scramble-contest spectrum. Scramble competition occurring when the limiting resource is widely dispersed, relatively abundant and thus non-monopolizable. At the other end is contest competition where these resources are more scarce or located in large patches and are more easily monopolizable (Janson & van Schaik, 1988).

1.13 Socio-ecology Model

As the 'ecological' sex female competition is over resources, and food distribution along with predation risk determines female social organization (Sterck et al., 1997). Males compete for access to fertile females, and female social organization, ubiquity, temporal distribution of fertility and ability to be monopolizable all provide the framework for male ranging and competitive behaviour (van Schaik & van Hoof, 1996). However, food distribution and/or predation can also play a role in male socio-ecology (van Schaik, 1983; Spillmann et al. 2017).

1.14 Male-male Competition

Male reproductive success is primarily being decided by contest competition over females, where paternity concentration is the ultimate, desired outcome. Over the course of their careers, optimal decision making, and socio-sexual strategies can vary depending on aspects of dominance over conspecifics, operational sex ratio (OSR), or female monopolization potential (van Noordwijk & van Schaik, 2004). A priority of access model (POA), dictates that the most dominant male gets the most attractive resource, with the next most attractive being available to the next ranked male (Altmann, 1962). Operational sex ratio is the proportion of fertile females to males and depends on female synchrony of fertility. An OSR skewed towards females due to heightened reproductive synchrony would lead to lower intensity of male-male contest competition (Emlen & Oring, 1977; Mitani et al., 1996). Lastly, female monopolization potential is determined by the OSR, as well as timing and duration of receptivity, and dictates the intensity of male-male competition. A high monopolization potential will create a highly skewed despotic society, with a lower monopolization potential showing less steep dominance ranks (van Noordwijk & van Schaik, 2001).

1.15 Loud Call

Male-male competition can be observed in primates in different ways, with physical confrontation being very intense, yet costly to both parties. One way to reduce these physical costs and mediate these dominance interactions is through long distance communication. In over 80% of forest dwelling primate species, males produce loud calls, and this loud calling behaviour is thought to be the ancestral condition in primates (Wich & Nunn, 2002). Loud calls can travel large distances due to their low frequency (Mitani et al., 1998) and correlate with home range size in some primates (Wich & Nunn, 2002). These multifunctional signals in primates encode content such as emotional arousal and environmental context (Galdikas & Insley, 1988; Norcross et al., 1999; Wich & Sterck, 2003, Rendall, 2003; Notman & Rendall, 2005; Spillmann et al., 2010, Salmi et al., 2013; Askew & Morrogh-Bernard, 2015) as well as convey individual identity (Wich et al., 2003; Rendall, 2003; Sproul et al., 2006; Delgado, 2007; Lameira & Wich, 2008; Spillmann et al., 2010; Askew & Morrogh-Bernard, 2015).

Specific acoustic parameters can function as an indicator of high genetic quality in other taxa, such as call duration in anurans (Welch et al., 1998; Doty & Welch, 2001) or call complexity and repertoire in avian species (Yasukawa et al., 1980; Mountjoy & Lemon, 1991). However, there is not yet an evident consensus on whether specific acoustic parameters consistently correlate with body size in primates, some studies find no correlation (Kitchen et al., 2003; Delgado, 2006; Ey et al., 2007), but others find vocal signaling can still reflect current condition, dominance rank or resource holding potential (Fischer et al., 2003; Benitez et al., 2016). Orangutan loud calls satisfy the requirements for a sexually selected signal (Snowdon, 2004; Delgado, 2006), and analysis of loud calls as a competition mechanism can serve to inform observers about the frequency, intensity and variation in male-male competition.

1.20 Orangutans (*Pongo spp.*)

1.21 Orangutan Socio-ecology

Several aspects of orangutan socio-ecology represent an atypical primate species. This semi-solitary, diurnal ape's social system can be described as 'individual-based fission-fusion' where non-discrete communities represent loose patterns of affiliation (van Schaik & van Hooff, 1996; van Schaik, 1999; Mitra Setia et al., 2009). However, in areas of Borneo with lowered forest productivity, these ecological constraints limit sociality and females tend to live more solitarily (van Schaik, 1999; van Noordwijk et al., 2009). Female orangutans are the philopatric sex and they live in stable, widely overlapping home ranges in proximity with their maternal kin (Morrogh-Bernard et al., 2011; van Noordwijk et al., 2012). Orangutans inter-birth intervals (IBI) can reach 7-7.5 years, marking the longest IBI found in all mammals (van Noordwijk et al., in press), and this along with non-advertised ovulation (Nadler, 1977; Galdikas, 1981) suggests fertilization opportunities are sporadic and infrequent for males.

In contrast, males engage in long ranged dispersal (Singleton & van Schaik, 2001; Nater et al., 2011). This is consistent with most other mammals showing a stronger philopatric tendency in females with male biased dispersal (Greenwood, 1980; Waser & Jones, 1983). The extent of this male dispersal and orangutan ranging is still not yet fully understood as there is considerable variation in male presence. Resident males are consistently seen at research sites over the course of a study year, whereas non-residents may pass through a study area once, and not be seen again until years later (Spillmann & van Noordwijk, unpub.).

Knowledge of home range size is also limited. Female home range estimates can be as low as 100-300 ha in areas of central and eastern Borneo (van Schaik et al., 2005; Morrogh

Bernard, 2009; Utami Atmoko et al., 2009; Buckley, 2014) or higher between 400-800 ha in western Borneo and Sumatra (Singleton & van Schaik, 2001; Knott et al., 2008). Males home range have been estimated to be anywhere between 300-1000 ha in central and western Borneo (Knott et al., 2008; Morrogh-Bernard et al., 2009; Buckley 2014) and up to 1500 ha in Sumatra (Singleton & van Schaik, 2001). However, these estimates are surely limited by field site size or study length and it may not be possible to accurately assess orangutan ranging by behavioural data collection alone. Aspects of forest productivity, and environmental homogeny may additionally play a role in home range variation and environmental usage. However, all home range studies agree that flanged male ranging behaviour is much more extensive and covers larger areas than adult females.

1.22 Orangutan Male-female Relationships

Flanged male orangutans are generally the most solitary age-sex class, with only some sites showing flanged males having regular, prolonged associations with females (MacKinnon, 1971; van Schaik & van Hoof, 1996; Mitra Setia et al., 2009). These longer term consortships in Sumatra can be associated with mast fruiting events, where individuals will travel between feeding patches together (Utami et al., 1997). Consortships can last for either a few days, or several weeks and can be initiated voluntarily through females or through chance encounters (Delgado & van Schaik, 2000). Orangutans are the only non-human primate in which forced copulations occur frequently (Knott & Kahlenberg, 2007; Muller & Emery-Thompson, 2012), and these elements of sexual harassment are seen in orangutan male-female relationships through coercive hand holding or extensive mate guarding. Females choice can play a role in sexual harassment counter-strategies by remaining within earshot of a dominant flanged male and approaching long calls to shake off harassing males (Fox, 2002; Mitra Setia & van Schaik, 2007).

1.23 Male Orangutans & Bimaturism

Among orangutans, there are two adult male morphs: flanged and unflanged. These male morphs are produced through unflanged males arresting their development, while flanged males have completed the irreversible, maturation process. This orangutan case of irreversible male bimaturism is the only one seen in primates. Different male morphs are seen in species such as mandrills *(Mandrillus sphinx)* (Wickings et al., 1992) or sifakas (*Propithecus verreauxi*) (Lewis & van Schaik, 2007), but these morphs reflect intrinsic condition, are reversable and not a case of arrested development.

Flanged males can be over twice the size of females representing not only the largest arboreal animal but also the highest degree of sexual dimorphism in primates (Leigh & Shea, 1995; Plavcan & van Schaik, 1997; Delgado & van Schaik, 2000). Their size is one of many conspicuous secondary sexual characteristics flanged males possess such as large fatty tissue flanges on the face, large laryngeal sacs, and long hair on the limbs and body. The laryngeal sac and flanges are thought to support long calling behaviour, as flanged males are the only age-sex class to utilize these prominent vocalizations.

Sexual selection acts on these two male morphs due to alternative reproductive tactics. Both of these adult male morphs are able to sire offspring, and males can remain unflanged for 20-30 years before developing into a flanged male (Utami Atmoko et al., 2002; Goossens et al., 2006; Lenzi, 2014). Flanged males compete more directly to monopolize females and sire offspring, while unflanged males try to force copulations, or sneak cooperative copulations during relative times of instability. While it has been called 'calling and waiting' in contrast to unflanged males who 'search and find' (Utami-Atmoko et al., 2009). This may not be the case in all sites, where recent work in Tuanan, Bornean show that flanged males do not necessarily 'call and wait' and instead can 'search and find' for fertile

females (Spillmann et al., 2017). The presence of mixed reproductive strategies through unflanged male arrested development is thought to be the evolutionary stable strategy (ESS). Where under higher levels of female monopolization potential, the unflanged male reproductive advantage is more pronounced (Pradhan et al., 2012).

1.24 Orangutan Male-male Relationships & Competition

Orangutan flanged male relationships exist in the context of intense competition and dominance hierarchies, and flanged males are extremely intolerant of other flanged males. Physical confrontations are common between flanged males (Dunkel, unpub.). While chases with unflanged males can occur, there are no recorded physical interactions between flanged and unflanged males in orangutans, and unflanged males even are occasionally tolerated in party contexts with adult females (Utami Atmoko et al., 2009). This could be explained by an inherit flanged male reproductive advantage (Mitani, 1985b) or that flanged males are the largest age-sex class and have higher locomotion costs, being slower than unflanged males. Flanged male interactions are present through chases or physical confrontations but are most common through long calling.

1.25 Orangutan Long Call

Flanged males exclusively emit the most prominent orangutan vocalization, the long call. While not particularly costly in energetics (Spillmann et al., in prep.), these vocalizations carry a potential social cost in attracting unwanted attention from a more dominant flanged male (van Schaik & van Hoof, 1996; Spillmann et al., 2017). This orangutan long call can be heard from over 1300 metres depending on terrain (van Schaik et al., 2013; Spillmann et al., 2017) but may be only individual recognizable within 300-400 metres (Mitra Setia & van Schaik, 2007; Lameira and Wich, 2008; Spillmann et al., 2016). They can last up to 5 minutes (pers. obs.) and are broadcasted indiscriminately, without a specific receiver.

There are two non-mutually exclusive hypotheses for the adaptive function of the male orangutan long call. First is to help females locate males, second is to mediate dominance hierarchies and repel other flanged males (Galdikas, 1983; Mitani 1985a). Within both hypotheses of the long call adaptive function, the purpose remains to coordinate movement with females (Fox, 2002; Mitra Setia & van Schaik, 2007) and other males (Mitani, 1985a) by announcing location. Intended daily travel direction is announced by long calls, and subsequent travel directions are updated as well (van Schaik et al., 2013; Askew & Morrogh-Bernard, 2015).

The contexts in which these long calls are given, such as spontaneous situations, or as an elicited reaction towards other long calls or forest sounds are detectable in the acoustic structure of Bornean flanged male long calls (Spillmann et al., 2010; Askew & Morrogh-Bernard, 2015). These different contexts of long calls may serve different functions, with spontaneous calls intended to attract females, and elicited calls functioning more towards male-male competition (Spillmann et al., 2010). These long calls reflect individual identity and competition motivation over intrinsic body condition (Delgado, 2003; Spillmann et al., in prep.), and consistent, quantifiable differences are found among individuals, populations and islands (Delgado, 2007).

1.26 Sexual Selection in Orangutans

There is strong evidence of sexual selection within orangutans and it plays a considerable role in their social organization and male-male competition. Elements of inter-sexual selection are seen through female mate choice. Females will remain within earshot of a locally dominant male (Fox, 2002), associate preferentially with a prime flanged male around times of ovulation (Knott et al., 2010) and attempt to resist males during periods of sexual harassment (Fox, 2002). Evidence of intense intra-sexual competition is found in extreme orangutan sexual and canine dimorphism (Plavcan & van Schaik, 1992; Plavcan & van Schaik, 1997) and the evolution of a flexible reproductive strategies through developmental arrest. Primate mating systems are shaped extensively by intense male-male competition (Mitani et al., 1996) and the geographic variation observed in orangutans offers a unique opportunity to study differential male competitive behaviour.

1.30 Geographic Variation in Orangutans

1.31 Orangutan Evolutionary History

~3.5 million years ago two of the extant species of orangutans diverged and now live on two distinct islands; Sumatra *(Pongo abelii)* and Borneo *(Pongo pygmaeus)* (Arora et al., 2010; Nater et al., 2011). The third species *(Pongo tapanuliensis)* diverged and became geographically isolated ~2.09 million years ago south of Lake Toba in Sumatra (Nater et al., 2011; Nater et al., 2017). Within *Pongo pygmaeus* there are 3 recognized subspecies, *P. p. pygmaeus, P. p. wurmbii,* and *P. p. morio*. These Bornean subspecies have surprisingly recent divergence estimates of ~176 kya given the deep evolutionary split of the two islands (Arora et al., 2010). This could indicate a recent bottleneck event in Borneo and subsequent repopulation of the island (Arora et al., 2010). Despite being related close enough genetically to produce viable offspring, Sumatran (*Pongo abelii*) and Bornean (*Pongo pygmaeus*) orangutans have marked differences in behaviour and ecology.

1.32 Ecology of the Islands

The rich volcanic soils of Sumatra support a more productive forest and a higher availability of soft pulp fruit (Marshall et al., 2009; Wich et al., 2011). As a result of this productivity, the highest population densities recorded in orangutans are found in Western Sumatran field sites, and lowest found in Eastern Borneo (Husson et al., 2009). This higher density in Sumatra leads to higher levels of gregariousness and sociability (Delgado & van Schaik, 2000; Mitra Setia et al., 2009). Sumatran orangutans come to the ground less than Bornean orangutans, perhaps due to the presence of terrestrial Sumatran tiger predation risk (Krutzen et al., 2011; Ashbury et al, 2015). The length of pulses and duration of the flanged male long call has been shown to differ between the two populations (MacKinnon, 1974; Delgado, 2007). These behavioral and ecological differences may contribute to different

competitive pressures on these two populations and are generally regarded as living under different social systems. If subsequent geographic variation in male competition behaviour exist, there should be quantifiable differences in flanged male long calling behaviour.

1.33 Sumatra (Pongo abelii)

The mating system in Sumatra is commonly described as having a 'locally dominate male' where orangutans form loosely associated, dispersed communities. This locally dominate flanged male forms longer voluntary consortships with females where they can monopolize matings (van Schaik & van Hoof, 1996; van Schaik, 1999; Delgado & van Schaik, 2000; Singleton & van Schaik, 2002). Female mate choice is seen in this preferential association with the locally dominant flanged male (Mitra Setia et al., 2009) by remaining within 'earshot' of the dominant flanged male long call range and approaching his long calls, potentially to reduce sexual harassment (Fox, 2002; Mitra Setia & van Schaik, 2007). However, this same male's long calls may be potentially ignored during their post-dominance tenure (Conradie, 2014).

These locally dominant males in Western Sumatra enjoy extended tenures, with an 18-year tenure reported for Jon in Ketambe (Utami Atmoko & Mitra Setia, 1995), or Suaq males such as Arno who remained dominant for > 6 years in the 90s (van Schaik, pers. comm.) or Islo who seemed preferred for > 4 years (Appendix: 5.0.3). Sumatran orangutans also exclusively travel through the trees, except in extenuating circumstances such as fights or fleeing. This increases overall locomotion costs and accentuates the difference in locomotion speed between flanged and unflanged males (Ashbury et al., 2015). This higher ranking, dominant male tends to long call, respond and approach long calls more often (Delgado, 2003; Mitra Setia & van Schaik, 2007). Male-male competition in Sumatra is considered to be a form of contest competition with stable dominance hierarchies.

The presence of a 'locally dominant male' mating system may contribute to the prevalence of developmental arrest in Sumatra, where the male morph ratio is biased towards unflanged males, who can outnumber flanged males by 2x in Sumatra (Dunkel et al., 2013). This alternative reproductive tactic may be more prevalent due to higher female monopolization potential (Pradhan et al., 2012) and a reduction in subordinate flanged males mating advantage, as subordinate flanged males and unflanged males are all subordinate to the locally dominant male.

This mating advantage is shown in paternal analysis of Sumatran infants, which demonstrate a high skew in paternities from the locally dominant male (Utami Atmoko et al., 2002; Lenzi, 2014). Whereas unflanged males secure paternities during periods of relative instability or with primiparous females (Utami Atmoko et al., 2002; Utami Atmoko et al., 2009). This locally dominant male system relies on high female monopolization and female choice to secure paternity concentration, and it is thought these males have a smaller home range than other, more transient males (Singleton & van Schaik, 2001).

1.34 Borneo (Pongo pygmaeus)

In Borneo, a 'promiscuous roving male' mating system has been described, where flanged males travel far and wide to find receptive females (Knott, 1998). This roving male system is associated with lowered home range fidelity, and repeated physical encounter costs (Reichard & Boesch, 2003). Bornean flanged males consortships with females generally do not last as long as Sumatran consortships (Delgado & van Schaik, 2000) and Bornean females with dependent offspring are shown to avoid spontaneous flanged male long calls (Spillmann et al., 2010). However, there may be some evidence for a female attraction function of long calls through sexually active females slightly approaching male long calls (Spillmann et al., 2010), and female choice through preferentially associating with more

dominant males during times of ovulation (Knott et al., 2010). Bornean flanged males also force copulations more frequently than flanged males in Sumatra (Mitani, 1985b; Utami Atmoko et al., 2009).

There seems to be a reduction in developmental arrest among Bornean males, which lends itself to a higher ratio of flanged males to unflanged males (Dunkel et al., 2013). This increase in competitors would support a lower female monopolization potential and suggest that the unflanged males reproductive advantage is limited (Pradhan et al., 2012; Dunkel et al., 2013). Additionally, terrestrial travel is more common in Bornean flanged males and these lower costs of locomotion allow more rapid and less conspicuous travel to engage in confrontations and competition (Wrangham, 1979; Ashbury et al., 2015).

An unstable contest competition mating system such as the 'promiscuous roving male' in Borneo would lend itself to a low-skew paternity outcome. Indeed, this is found in northeastern Borneo, Kinabatangan (Goossens et al., 2006). However, brief periods of flanged male paternity concentration are found in central Borneo, Tuanan (van Noordwijk, unpub.), northeastern Borneo, Kabili Sepilok (Tajima et al., 2018) or southern Borneo, Tanjung Puting where Kusai, a local male had a ~10-year dominance tenure and secured concentrated paternities over that time period (Banes et al., 2015). However, Tanjung Puting also serves as a rehabilitation and release site, and local orangutans are provisioned medicinally and with food, which may change factors of male condition related to extended tenures of dominance and female monopolization.

A closer inspection of flanged male competition through the long call mechanism found a 'confrontational assessment' system in central Borneo, Tuanan (Spillmann et al., 2017). Where males roam due to fruit availability, but compete through long calls selectively, depending on receptive females being present, or other flanged males. These Bornean flanged

males assess each other through long call confrontations to update individual status and determine competition motivation (Spillmann et al., 2017).

1.35 Previous Work

Research done on orangutan long calls have primarily been focused on naturalistic and play back experiments focused on immediate and delayed ranging response, as well as long call structure analysis to determine individual identity or emotional arousal (Mitani 1985a; Delgado, 2003; Mitra Setia & van Schaik, 2007; Lameira & Wich, 2008; Spillmann et al., 2010; Conradie, 2014; Askew & Morrogh-Bernard, 2015). While passive acoustic monitoring techniques have become more common in cetacean (Mellinger et al., 2007; Thomas & Marques., 2012), anuran (Swiston & Mennill, 2009; Celis-Murillo et al., 2012), and even elephant studies (Wrege et al., 2010; Wrege et al., 2012) few primate studies have utilized these methods (Kalan et al., 2016) with even fewer utilizing an Acoustic Localization System (Spillmann et al., 2015, 2017). This thesis will use this novel approach of passive data collection in Bornean and Sumatran orangutans to explore geographic variation of orangutan competitive behavior through the long call mechanism.

1.40 Research Objectives

We aim to test male-male competition systems in two species of orangutans, operating under two different mating systems. We expect to find marked differences in competition behavior through the long call mechanism due to the 'locally dominant male' mating system in Sumatran orangutans (*Pongo abelii*). While there seems to be no locally dominant male currently in the Suaq, Sumatra field site, we don't expect to find the same confrontational assessment approach found in Bornean flanged males (*Pongo pygmaeus)*, due to the perceived increased stability of male dominance hierarchies in Sumatra.

1.41 Research Questions & Predictions

1) Which research site has more flanged males present in the area?

Prediction: Due to the 'promiscuous roving male' mating system described in Borneo, and the reduction of developmental arrest in Bornean orangutans (Dunkel et al., 2013), we expect to find more males at the Tuanan, Borneo research site roving through, as well as more calling males within the ALS grid on a daily basis.

2) Does fruit availability dictate Suaq, Sumatran male ranging behaviour?

Prediction: In the 'confrontational assessment' model of male-male competition in Tuanan, Borneo, flanged male presence in an area is determined by fruit availability (Spillmann et al., 2017). With the consistently higher fruit availability in Sumatra compared to Borneo (Marshall et al., 2009; Wich et al., 2011), we don't expect to find an effect on calling male presence from fruit availability in Suaq, Sumatra.

3) Which research site has more silent males?

Prediction: If dominance hierarchies in Sumatra are more stable, we expect males to confront each other less often. We would then expect to see more non-calling males in Suaq, Sumatra compared to Tuanan, Borneo.

3) Is there a difference in daily call rates between the sites?

Prediction: With the surplus of flanged males in Borneo (Dunkel et al., 2013) and 'confrontational assessment' model of male-male competition (Spillmann et al., 2017) we expect that Tuanan, Bornean males long call more than Suaq, Sumatran males.

4) Is there a difference in daily response rates between the sites?

Prediction: Under the 'confrontational assessment' model of male-male competition, males confront each other based on identity and competition motivation. If more males are roving through, and dominance hierarchies are instable, than more confrontation is expected. We would then expect to see more long calls being responded to in Tuanan, Borneo.

5) Is there a difference in long call response latency?

Prediction: If latency can be inferred as emotional arousal, we would expect that Tuanan, Bornean flanged males respond to long calls quicker.

6) Is there a correlation between call rates and response rates in Suaq, Sumatra?

Prediction: In Tuanan, Bornean, flanged males who have higher call rates also have higher response rates. We expect to find the same in Suaq, Sumatra, higher call rates correlating with higher response rates.

2.0 Methods

2.10 Study Sites

This study compares behavioural and acoustic data from two different populations of orangutans (Figure 2.1.0): The Suaq Research Site located in South Aceh, Sumatra, Indonesia (*Pongo abelii*) and the Tuanen Research Site located in Central Kalimantan, Borneo, Indonesia (*Pongo pygmaeus wurmbii*).

Figure 2.1.0: Map of Indonesia with the research sites of this study outlined.

2.11 Suaq, South Aceh, Sumatra

Suaq (03°01'87''N; 97°25'01''E) is in the Gunung Leuser Nasional Park and the study area covers approximately 750 ha. The core study area is coastal peat swamp forest, with adjacent areas of mixed dipterocarp and riverine forests. The orangutans of Suaq have been habituated and observed from 1992 to 1999, then again from 2007 until present. Suaq has the highest density of recorded orangutans at 4 -7.44 individuals per km² (van Schaik et al., 2001) as well as a comparatively higher fruit availability (Hussons et al., 2009; Wich et al., 2011).

2.12 Tuanan, Central Kalimantan, Borneo

Tuanan (02°09'06''S; 114°26'26''E) is located within the Mawas Reserve and the study area covers over 1300 ha. The core study area is also comprised of peat swamp forest, however adjacent areas are comparatively more homogenous than at Suaq. In the past this area was subjected to selective logging and is currently regenerating, but presence of forest fires has made some areas of the Tuanan research site currently uninhabitable for orangutans. The Tuanan research site has had consistent researcher presence from 2003 until present. Orangutan densities are comparatively lower here, estimated at 4.25 – 4.50 individuals per km² (van Schaik et al., 2005).

2.20 Behavioural Data Collection

2.21 Focal Follows

Behavioural data was collected using full day focal follows of individually-recognized orangutans. Orangutans were followed over their entire diurnal activity period from morning nest to evening nest. Focal follow data was collected following the standardized orangutan research protocols by the University of Zurich to encourage data consistency and collaboration ability, this protocol includes both sampling technique and ethogram (http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html). Due to inconsistent orangutan availability, there was no set follow schedule and focal animals were followed opportunistically, and over consecutive days until the focal was lost or a maximum of 10 days per month were recorded. Individual identification was possible due to photos taken during focal follows to be compared with the Suaq orangutan identification database, and fecal samples for DNA analysis were taken whenever possible.

2.22 Long Call Sampling

During focal follows for every age-sex class all long calls heard were documented using all-occurrence sampling. During flanged male follows all long calls given were additionally documented. For every long call documented, parameters of time, duration, pulses, snag crash, estimated distance and direction were taken, as well as focal follow and all association partners reaction to the long call.

2.23 Active Long Call Recordings

Long call recordings were taken using an active, shotgun microphone (Sennheiser ME67) and a recording device (Zoom H2N). These long call recordings were taken at all occurrences during every flanged male focal follow.

2.24 Global Positioning System (GPS) Data

Handheld Garmin GPS units were used to record focal follow ranging behaviour, all long call occurrences, all nesting locations as well as locations where the focal was found or lost. State behaviour was recorded at half hour intervals, with feeding trees recorded if the focal spent over 5 minutes feeding in the same tree. Location and direction (cardinal degree) of long calls given were recorded for flanged male focal follows. Long calls heard were recorded at all-occurrence for all age-sex class follows, with estimated direction (cardinal degree) and distance (metres). The location of the beginning of all focal follows were recorded through morning nest location or where the focal was found. The end of the focal follow was also recorded through evening nest or where the focal was lost.

2.30 Acoustic Localization System (ALS)

The Acoustic Localization System (ALS) is a methodology developed by Brigitte Spillmann (2017) to record all flanged male orangutan long calls in space and time in Tuanan, Borneo. It consists of a fully autonomous, GPS time synchronized microphone grid that records continuously day and night and allows for localization and identification of long calls. This study replicates this methodology in Suaq, Sumatra.

2.31 Long Call Recordings

For this study, 16 passive acoustic recording devices (13 SM2 / 3 SM3 autonomous digital field recorders, Wildlife Acoustics) were installed in a grid with inter-microphone distances of 500 metres. While this ALS records continuously, manageable file sizes were ensured by running these recorders in 1h:57m blocks starting from 05:00 until 17:00, with a 3-minute gap being necessary for the recorder to consolidate the last recording file, before starting the next. So that the entire grid did not stop recording for these 3 minutes, each recorder start time was offset at 3-minute intervals (05:00, 05:03, 05:06, 05:09) to ensure complete forest coverage during the day. Overnight the recorders ran in 2h:30m blocks from 19:00 until 02:30, however each recorder only ran during one of these blocks each night, and thus night long calls are recorded but not localizable. This ALS supplemented focal follow vocalization recordings and behavioural data collection.

The Suaq data set for this study came from ALS data collected over 4 months (September 2016 – January 2017) using 16 recorders covering 2.25 km^2 (Figure 2.3.0). The Tuanan portion of the data set was previously collected and analyzed over 10 months (March 2012 – December 2012) using the full 20 recorder grid covering 3.0 km^2 (Spillmann et al., 2017). Before analyzing these ALS recordings, long calls must first be extracted, localized and identified.
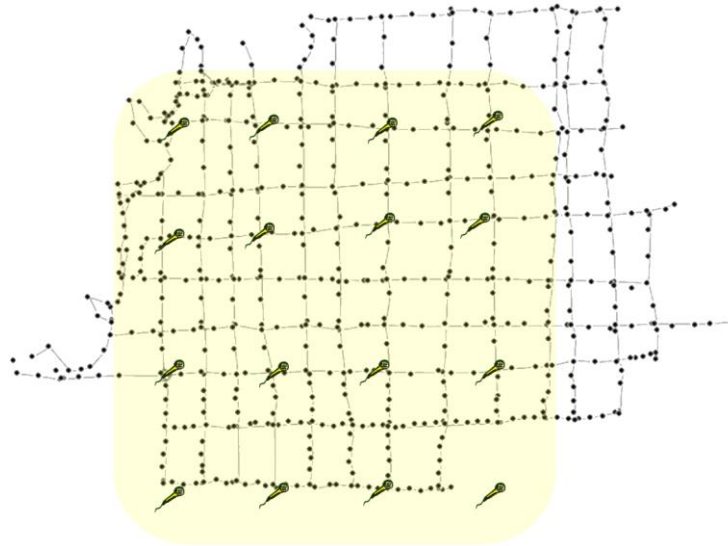
Figure 2.3.0: Map of the Acoustic Localization System in Suaq, Sumatra with localization area.

2.32 Long Call Extraction

Long call extraction was done using a trained recognition algorithm developed for Bornean flanged males long calls (Spillmann et al., 2015) in the software Songscope (Version 4.1.5). This algorithm scanned the ALS data files and left tags for every long call it found. These tags are then checked by a human observer, who then recorded long call start time, estimated distance from the record based on long call quality/loudness, possible idiosyncrasies in the long call structure, and if background noise masked this long call, following the same criteria as Spillmann et al. (2015). Algorithm quality and score can be adjusted to determine how 'choosy' these tags are matched, with quality representing quality of the recording, and score representing how closely these recordings match the algorithm. A quality of 64, and a score of 60 were used after ensuring that these settings would find long calls that were observed during focal follows but were sufficiently high enough to limit the number of false positives it would generate.

This extraction algorithm was validated by reviewing 95 long calls directly documented over 16 flanged male focal follows from 3 individuals (Islo, Xenix and Pluto). This algorithm at these settings found 93 of the 95 long calls resulting in a success rate of 98%, matching the 99% success rate from the Tuanan ALS data set. Because two different observers extracted long calls from the Suaq and Tuanan ALS data set, an inter-observer reliability test (IOR) was conducted. Data sharing between observers was deemed acceptable after an overall index of concordance of 90 and 95% was found for long calls determined to be Close and Medium distance to the recorder (Appendix: 5.1.4). Further information about the IOR can be found in Appendix: 5.1.3.

2.33 Long Call Localization

Localization of the long calls recorded was possible due to the ALS grid being time synchronized via a GPS satellite clock. This localization was performed in a custom Acoustic Platform developed specifically for this ALS grid by Spillmann and Walker to act as a long call database. Localizations were done through a cross-correlation of the long call's time of arrival between multiple recorders. The long call location was then plotted through triangulation of these time of arrival differences. A minimum of 3 recorders is necessary to perform this cross-correlation, and parabolas were generated where the long call was placed at the site of most overlap (Figure 2.3.1). While the Suaq 16 recorder grid covered only 2.25 km^2, it is possible to localize long calls occurring ~200 metres outside of the grid for a total localization area of 3.6 km^2. This 200 metre rim of extra localizing area is also found in the Tuanan ALS data for a localizing area of 4.5 km^2 . While the 20-recorder grid in Tuanan could record long calls from a total of 9.0 km^2, only long calls occurring within these localizing areas were used for this study.
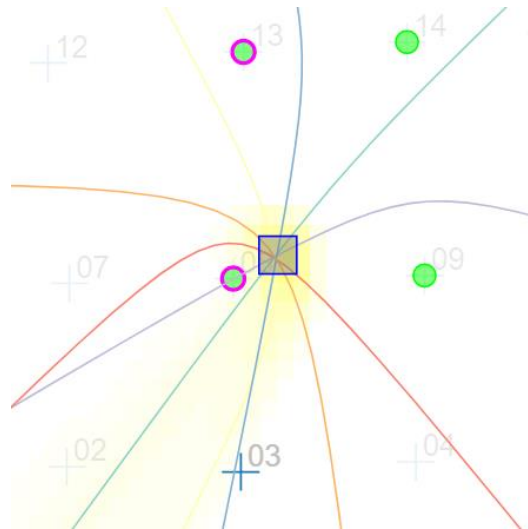
Figure 2.3.1: Example of one long call localization in the Acoustic Platform. Circles are recorders used for the localization. Individual parabolas indicate pair-wise cross-correlations where the long call may be located. Square is the most likely long call location, where there is the most parabola overlap.

This localization procedure was validated by comparing these Acoustic Platform localization points to GPS points of long calls given from flanged male focal follows. For the Suaq data set, an overall mean localization error of 56 metres was calculated from comparing 95 long calls. This compares favorably to a mean localization error of 59m from the Tuanan ALS data set. Further information on the long call localization procedure and validation can be found in Spillmann et al. (2015).

2.34 Long Call Identification

Determining flanged male identities for a particular long call was possible on a daily basis due to two different methods. First, using long calls from flanged male focal follows individuals can be directly identified via pictures. Second, a time-distance rule was used to link long calls to the same male that occured within 400m and 6 hours, with an additional parameter of not exceeding a maximum speed of 0.1 metres/second. This allowed pseudo-ids to be assigned on a daily level and daily long call and response rates to be analyzed. This time-distance rule was developed empirically using a combination of focal follow and ALS data to see what change in time and distance occurs between subsequent long call. The distance of 400 metres was chosen to limit the number of false positives (5) and negatives (1) it would generate out of 141 known long calls, with a success rate of 96% (Appendix: 5.1.5).

2.35 Long Call Parameters

Long call duration was recorded for all long calls through the Acoustic Platform, measured from the start of the first pulse to the end of the last pulse, bubbles and grumbles were not included. Measurements of long call pulse rate were taken in Raven Pro (Version 1.5) through the first ten pulses of each long call. For all active recordings of long calls from flanged male focal follows pulse rate was measured. Long call pulse rates were also measured from the ALS long call data set; all long call responses within 40 minutes and within 1300 metres, all long calls associated with a snag crash and a random sampling of spontaneous long calls (no long calls in 2 hours before, no snag crashes associated with call).

2.40 Behavioural Data Definitions

2.41 Fruit Availability Index (FAI)

Fruit availability indexes were calculated from both field sites on a monthly basis from phenology plots following a standardized University of Zurich protocol (http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html). FAI is defined as the proportion of monitored trees carrying fruit.

2.42 Proportion of Female Party Time

The time flanged males spent in association with females was measured and calculated as a proportion for both field sites. All available male-female associations were used for Suaq. The Tuanan data set calculated male party members from female focal follows for five individuals with the largest data sets Jinak, Mindy, Kerry, Juni, and Kondor.

2.43 Resident vs Visitor Males

Individual male presence per month over the course of a year was recorded from presence/absence data. If a male was seen 6 months or more in a single year, they were categorized as a resident male. Males seen less than 6 months were categorized as visitors.

2.44 Silent Males

Silent male follows were defined if there were no long calls given from the flanged male focal individual during the entire follow. Only follows over 5 hours were taken for this analysis. The proportion of silent follows / total follows, as well as unique silent males / unique males were calculated on a yearly basis.

2.45 Long Call Response Definitions

Responses were defined as a long call that occurred within 40 minutes of a previous long call from a different individual, at a maximum of 1300 metres away. Provoking long calls were defined as any long call that provoked another long call from a different individual within 40 minutes and 1300 metres.

2.50 Data Analysis

2.51 ALS Daily Long Call & Calling Males

In order to test these site differences in calling male presense and overall long call rates, two generalized linear models (GLM) were fitted. For each model I used daily calling males or daily long calls with site as the predictor variable, and fruit availability (FAI) as a fixed effect. Due to the different localization areas between the two grids, the km^2 was set as an offset for the daily calling males and daily long call models. Initially these model families were set to Poisson, to account for the non-normalcy of count data. However, model diagnosis showed unaccounted for variance and overdispersion. Based on this the family was then set to negative binomial with a theta of 1.

These models were calculated using R 3.4.2 (R Core Team, 2015) and the lmerTest (Kuzenetsova et al., 2017) and MASS (Veneables & Ripley, 2002) packages.

2.52 ALS Long Calls per Calling Male

Differences in individual long call behaviour between the sites was also tested using a GLM. Daily long calls were again the outcome variable, predicted by site, with FAI as a fixed effect. For this analysis the offset was set to daily calling males. This family was also set to negative binomial with a theta of 1.

This model was calculated using R 3.4.2 (R Core Team, 2015) and the lmerTest (Kuzenetsova et al., 2017) and MASS (Veneables & Ripley, 2002) packages.

2.53 ALS Long Call Responses

To test for differences in long call response behaviour, a GLM was fitted. The outcome variable was daily responses, with the site as the predictor variable. FAI was included as a fixed effect, and daily spontaneous long calls were set as an offset to control for the difference in overall call rates between the sites. The family was set to negative binomial with a theta of 1.

This model was also calculated using R 3.4.2 (R Core Team, 2015) and the lmerTest (Kuzenetsova et al., 2017) and MASS (Veneables & Ripley, 2002) packages.

2.54 Long Call Pulse Rates

An additional GLM was fitted to see if long call context could be predicted from long call pulse rate alone, within three individual males. Long call context was set as the outcome variable, and pulse rate as the predictor variable with individual identity as a random effect.

This model was calculated using R 3.4.2 (R Core Team, 2015) and the mblm (Komsta, 2013) package.

3.0 Results

3.10 Data Set

Table 3.1.0: Raw data used for this analysis, in terms of days extracted from the ALS data, total long calls, responses, and daily calling males. Tuanan data from Spillmann et al. (2017).

	Suaq	Tuanan
LC Days	76	108
Long Calls	581	1615
Responses	22	152

In total, 76 Suaq days of long call activity were analyzed based on the full 16-recorder ALS grid being active. This was compared against a 108-day sample of Tuanan long call activity from Spillmann et al. (2017). These 76 days in Suaq totaled 581 long calls, of which 22 were long call responses, versus 1615 total long calls, 152 of them being responses in Tuanan.

While 581 long calls from Suaq were sampled for the data analysis, 787 long calls were recorded over the 4 months in the localizing area, and a total of 1001 diurnal long calls altogether. This ALS additionally recorded 126 nocturnal long calls.

Over this 4 months in Suaq, there were 35 flanged male focal follows of which 17 were nest to nest. This resulted in 132 documented long calls given of which 87 were recorded with a shotgun microphone at close range. An additional 64 long calls heard were documented from all age-sex class focal follows. Human observation through focal follows captured 196 long calls over the same time period when 787 long calls actually occurred in the research area.

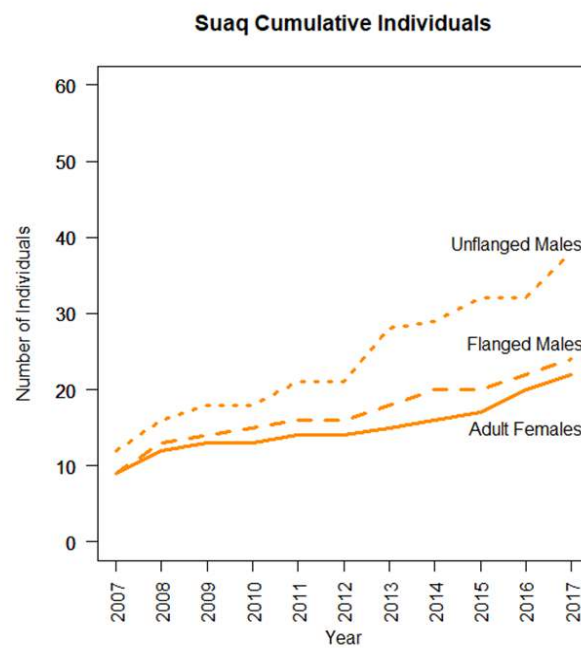## 3.20 Behavioural Data

3.21 Flanged Male Presence

Figure 3.2.0: Cumulative adult individuals over time in Suaq separated by age-sex class.
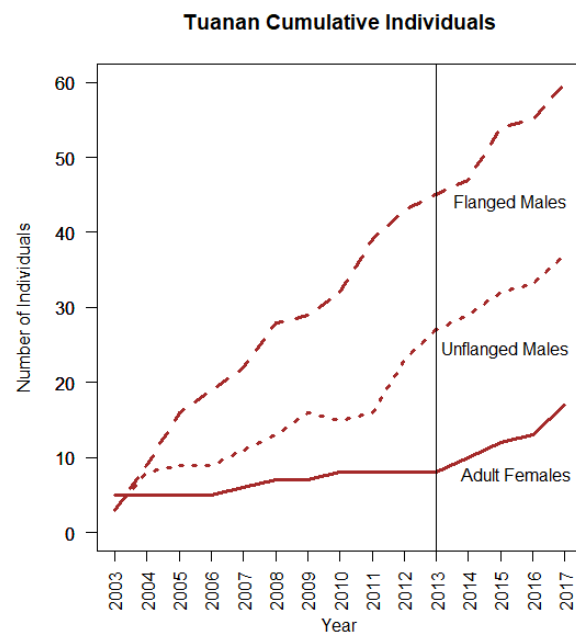

Figure 3.2.1: Cumulative adult individuals over time in Tuanan separated by age-sex class. Vertical line marks ten years of study.

In Tuanan, there are more males passing through the study area than in Suaq. There have been 24 unique flanged males individuals identified over the 10 years of study in Suaq (Figure 3.2.0), compared to 45 flanged males over the first 10 years in Tuanan (Figure 3.2.1). In total, 60 flanged males have been seen over the 15-year study period in Tuanan.

This surplus of flanged males in Tuanan compared to Suaq is also seen in ratios of unique individuals recorded per year by age-sex class. The socionomic sex ratio of flanged males to adult females show a clear flanged male bias in Tuanan, not seen in Suaq (Figure 3.2.2). There is also an apparent flanged male bias in Tuanan when measuring male morph ratios of flanged males to unflanged males (Figure 3.2.3).

Flanged males seem to be the most prevalent age-sex class yearly in Tuanan, in terms of unique individuals per year (Appendix: 5.0.6), compared to Suaq which has frequently more unique adult female individuals and unflanged males per year (Appendix: 5.0.5).
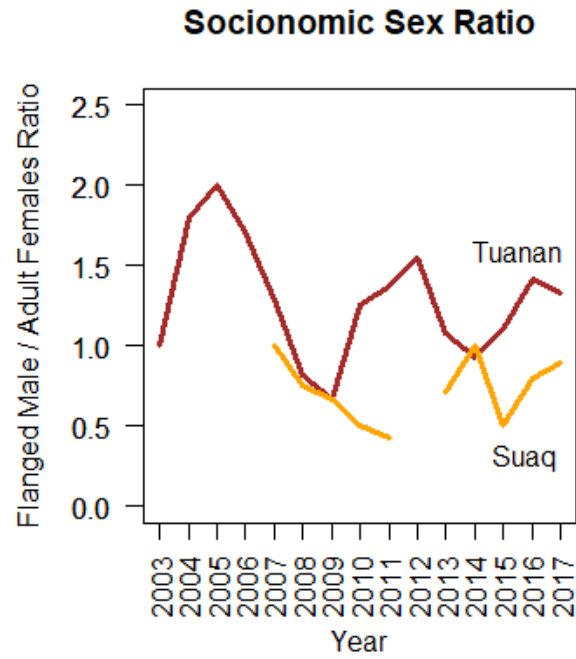
Figure 3.2.2: Socionomic sex ratio of flanged males to adult females, measured in unique individuals sighted per year.
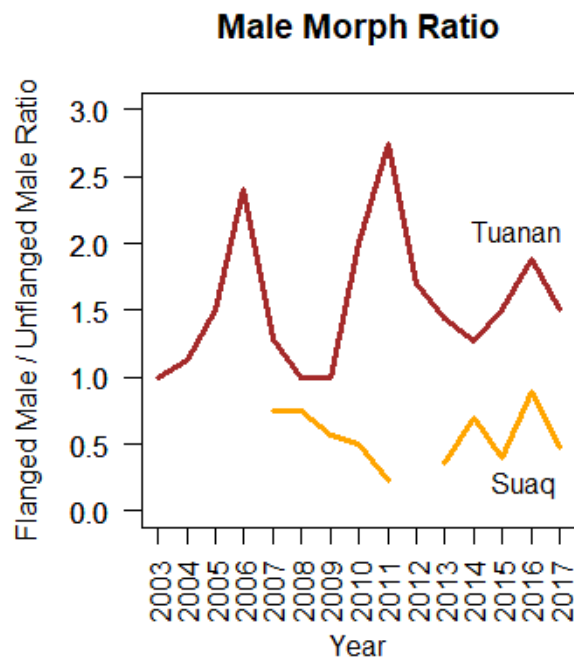

Figure 3.2.3: Male morph ratio of flanged males to unflanged males, measured in unique individuals sighted per year.

3.22 Proportion of Female Party Time

Evidence of a preferred flanged male is found in the proportion of party time spent with females. Early years in Suaq show a clear preference for one flanged male Islo, which declines until 2014. This decline timeline matches observations of repeated facial wounds on Islo, starting in January 2014. Afterwards Titan had one year as the preferred flanged male, with Islo returning for one more year. Since there doesn't seem to be one clearly dominant male in Suaq in terms of proportion of female party time (Appendix: 5.0.3).

Islo is responsible for over half of the yearly residential male sightings seen in Suaq (Appendix: 5.0.7). There were 6 instances of a unique residential male in the Suaq study area and 4 of those came from Islo. Every study year he was present over 4 months of the year until 2015 (Appendix: 5.0.1)

These extended tenures of preferred female associations are not seen in Tuanan (Appendix: 5.0.4). While there are residential males that are seen in the area in over 6 months in a year (Appendix: 5.0.8), none seem to enjoy these extended tenures of preferred female association seen in Suaq.

3.23 Silent Males

Table 3.2.0: Mean yearly proportion of silent follows out of total yearly follows, and mean proportion of silent males out of unique males per year.

	Suaq	Tuanan
Proportion of Silent Follows	0.35	0.42
Proportion of Silent Males	0.24	0.22

A Mann-Whitney U test indicated that there is no difference in silent follows in Tuanan compared to Suaq (U=87, p = 0.52). There is additionally no significant difference in silent males between the two sites (U=86, p = 0.57) (Table 3.2.0). Full tables for yearly measures of silent follows and males in Suaq (Appendix: 5.1.6) and Tuanan (Appendix: 5.1.7) are available in the appendix.

3.30 Acoustic Localization System

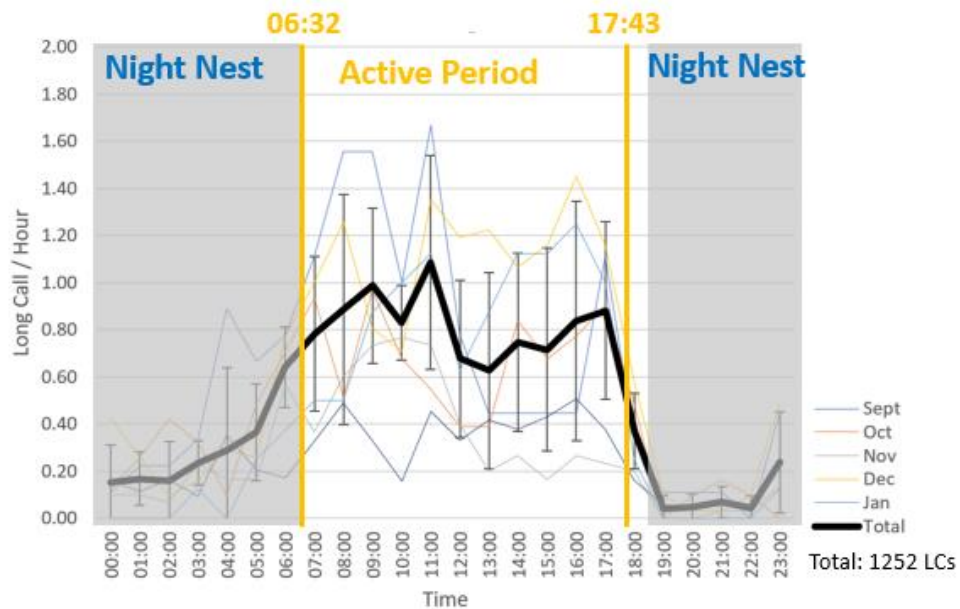## 3.31 Circadian Distribution of Long Calls

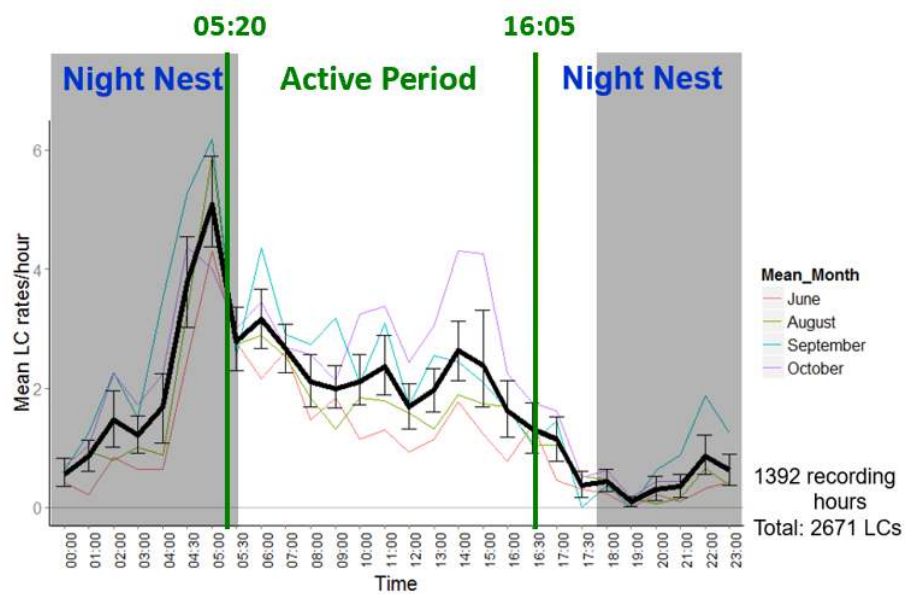**Figure 3.3.0:** Circadian distribution of long call rates in Suaq.

Figure 3.3.1: Circadian distribution of long call rates in Tuanan.

There are differences in daily long call usage when looking at the circadian distribution. In Suaq, call rates increase gradually until the late morning, drop, and then gradually increase until another slight pre-dusk calling peak (Figure 3.3.0). There is not a clear peak of increasing call rates within a small window of time, as seen in Tuanan. Tuanan males show a distinct pre-dawn calling peak where call rates increase by ~2.5x, then long call activity trails off during the day (Figure 3.3.1).
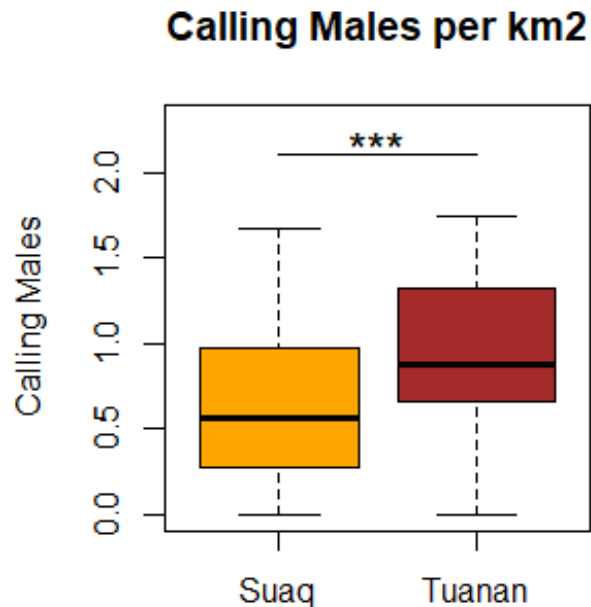
3.32 Daily Calling Males

Figure 3.3.2: Calling males per km^2 for Suaq and Tuanan.

Table 3.3.1: GLM results for calling males within the ALS grid predicted by site, with fruit availability as a fixed effect and offset for respective localizable area.

Response	Effect	Effect type	Estimate	Std-Error	T Value	P Value	N Est.	N Total
Calling Males	Site(Tuanan)	Fixed	0.90	0.15	6.09	**< 0.001**	2	192
per km²	FAI	Fixed	0.07	0.01	4.97	**< 0.001**	2	192

On a daily basis, more calling males pass through the recorder grid in Tuanan compared to Suaq, adjusted for recorder grid size (Figure 3.3.2). The average daily calling males per square kilometre for Suaq is 0.69 (+/- 0.45) versus a mean of 0.93 (+/- 0.39) in Tuanan. However, the max amount of amount of calling males seen in the area is similar between the two sites, 1.67 for Suaq and 1.75 for Tuanan. This difference in calling males per square kilometre proves to be statistically significant (F=0.30 , p=<0.001) between the two sites, with a positive effect towards Tuanan (Table 3.3.1).
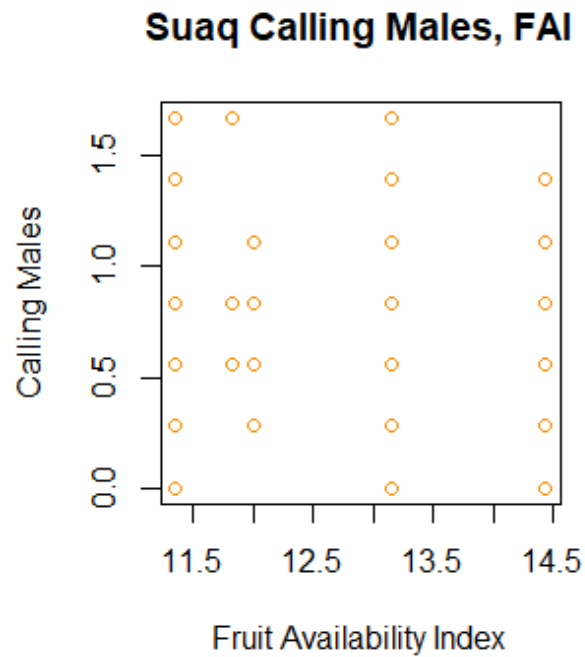
3.33 Effects of FAI on Daily Calling Males

Figure 3.3.3: Daily calling males within Suaq, plotted against fruit availability.
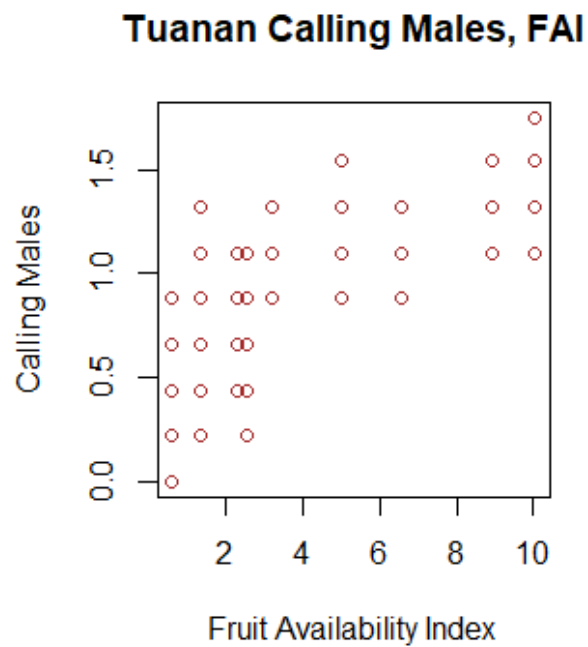

Figure 3.3.4: Daily calling males within Tuanan, plotted against fruit availability.

Table 3.3.2: Spearman's correlation results between calling males and fruit availability, at Suaq and Tuanan.

Calling Males, FAI	rho	p-value
Suaq	-0.21	0.056
Tuanan	0.70	**< 0.001**

Suaq calling males presence in the ALS grid does not seem to be affected by fruit availability (rho = -0.21, p = 0.056). However, within the Tuanan research area the presence of calling males within the ALS grid does seem to be driven primiarily by fruit availability. These two variables correlate significantly (rho = 0.70, p = <0.001). With increasing fruit availability, there are more calling males seen daily within the the ALS grid in Tuanan (Table 3.3.2).

However, the ALS data set from Suaq covered a shorter period of time (4 months), and much smaller FAI range (11.35 – 14.43), than the Tuanan data over 10 months with a larger FAI range (0.572 – 10.05). Without periods of lowered fruit availability in the Suaq data set, it is difficult to assess fully the impact of FAI on male ranging.
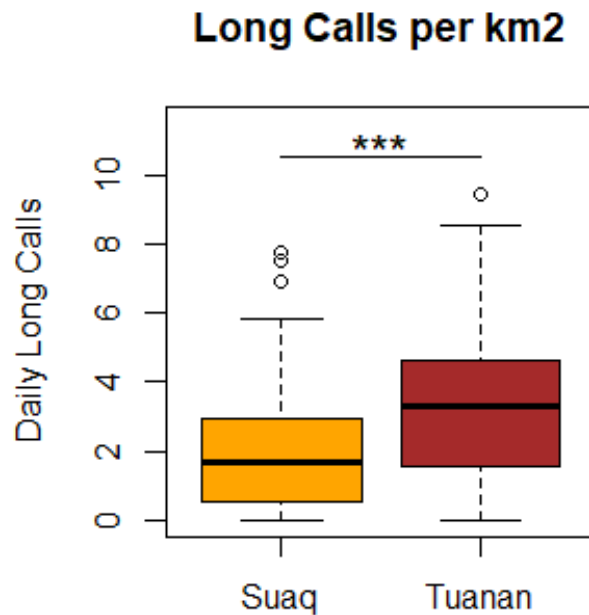
3.34 Daily Long Calls

Figure 3.3.5: Daily long calls per km^2 for Suaq and Tuanan

Table 3.3.3: GLM results for long calls within the ALS grid predicted by site, with fruit
availability as a fixed effect and offset for respective localizable area.

Response	Effect	Effect type	Estimate	Std-Error	T Value	P Value	N Est.	N Total
Long Calls	Site(Tuanan)	Fixed	1.18	0.22	5.47	**< 0.001**	2	192
per km²	FAI	Fixed	0.10	0.02	4.78	**< 0.001**	2	192

There are more long calls occurring in Tuanan compared to Suaq. Suaq's mean daily

long call per km^2 is 1.91 (+/- 1.88) compared to Tuanan's mean daily longs calls per km^2 of

3.25 (+/- 2.03) (Figure 3.3.5). Suaq's daily maximum is 7.78 long calls occurring in a square

kilometer, with Tuanan's being 9.43. In Suaq, there was 7 days with 0 long calls, and a

further 10 days with only 1 long call occurring within the grid, while there was only one day

during the ALS coverage in Tuanan where 1 long call or less occurred in Tuanan.. The results

of the GLM indicate that study site is a significant predictor of long call activity, with a

positive effect towards Tuanan (F=0.44, p=<0.001) (Table 3.3.3).
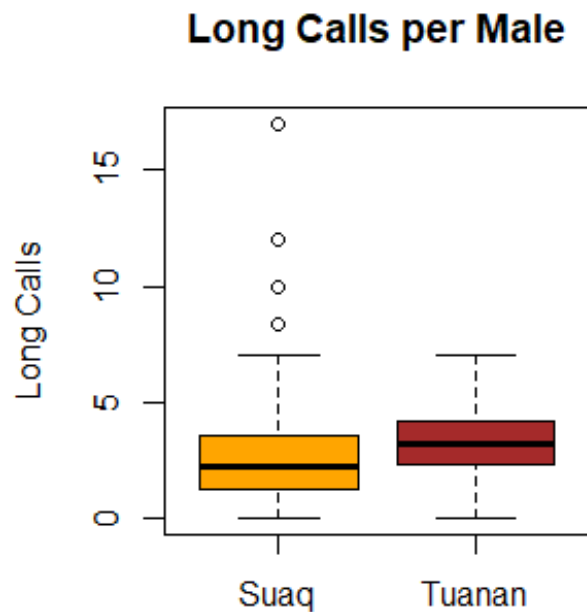
3.35 Long Calls per Calling Male

Long Calls per Male

Figure 3.3.6: Long calls per male for Suaq and Tuanan.

Table 3.3.4: GLM results for long calls within the ALS grid predicted by site, with fruit availability as a fixed effect and offset for respective number of calling males.

Response	Effect	Effect type	Estimate	Std-Error	T Value	P Value	N Est.	N Total
Long Calls per	Site(Tuanan)	Fixed	0.28	0.18	1.64	**0.103**	2	192
Calling Male	FAI	Fixed	0.02	0.02	1.59	**0.113**	2	192

Although there is more males and more long calls in Tuanan, these males are giving similar amounts of long calls per day (Figure 3.3.6). Suaq males average 2.90 long calls per day (+/- 2.65) while Tuanan males averages 3.31 (+/- 1.41). This difference in long calls per males between the sites is not statistically significant (F=0.06, p=0.491). This difference in long calls per km^2 seems to be driven primarily through the abundance of flanged males in Tuanan. There are prominent outliers in the Suaq dataset, caused by one calling male in the area alone, calling a max of 23 times in a single day.

3.36 Correlation Between Calling Rates & Response Rates

Table 3.3.5: Spearman correlation results for Suaq males' individual call rates correlated with response rates, and provocative long call rates.

Individual Spontaneous Call Rates	rho	p-value
Response Call Rates	-0.04	0.781
Provoking Call Rates	0.05	0.702

While there are instances of high daily calling rates within the Suaq recorder grid, there is no correlation between heightened daily call rates, and response (rho = -0.04, p = 0.781) or provocative call rates (rho = 0.05, p = 0.702) (Table 3.3.5). Neither is there a correlation between response rates and provocative call rates. Suaq males with higher call rates are not responding to more long calls or provoking more responses from other males. This result contrasts with Tuanan where there is a correlation between call rates and response rates, where higher calling males are also responding to more long calls.
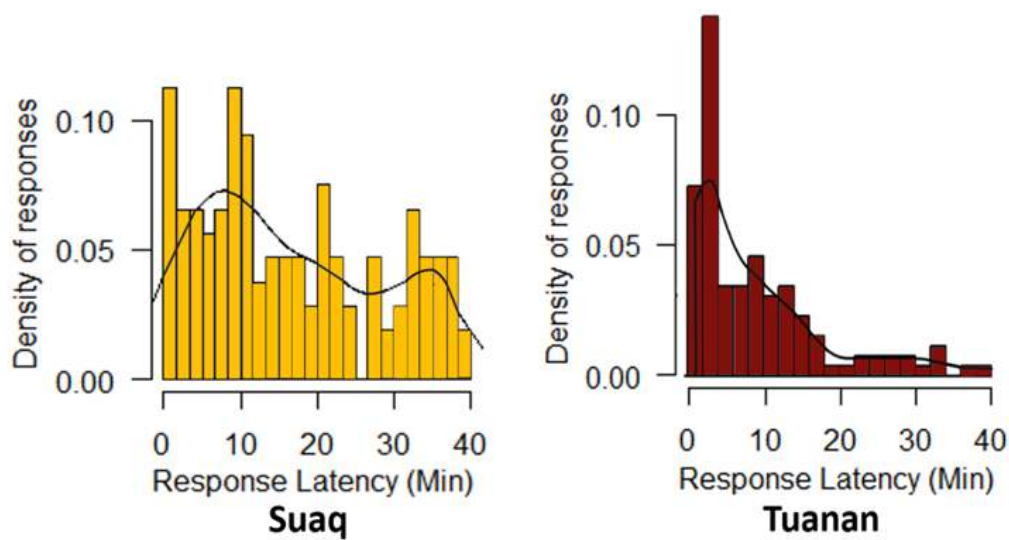
3.37 Long Call Response Latency

Figure 3.3.7: Frequency histograms of Suaq & Tuanan long call response latencies.

Tuanan flanged male responses occur at a more immediate latency rather than Suaq (Figure 3.3.7). In Tuanan the majority of responses occur within 5 minutes of the provoking long call , however in Suaq a different, more relaxed pattern is found. While it seems, there is a 10-minute window for an immediate long call response, it's not uncommon for long call responses to occur outside of 20 minutes.
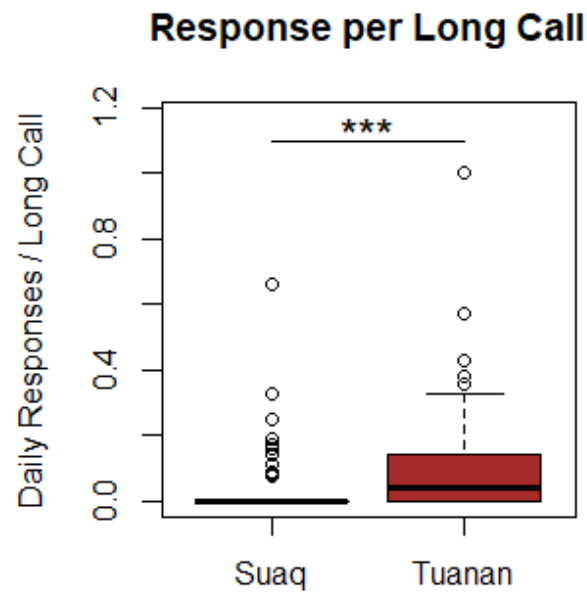
3.38 Responses per Long Call

Figure 3.3.9: Responses per long call for Suaq and Tuanan.

Table 3.3.6: GLM results for responses within the ALS grid predicted by site, with fruit availability as a fixed effect and offset for respective long call rates.

Response	Effect	Effect type	Estimate	Std-Error	T Value	P Value	N Est.	N Total
Responses	Site(Tuanan)	Fixed	1.80	0.42	4.33	**< 0.001**	2	192
per Long Call	FAI	Fixed	0.11	0.04	2.69	**0.007**	2	192

Flanged males in Tuanan respond to more long calls than males in Suaq. The mean amount of daily long calls responded to in Suaq is 0.03 (+/- 0.09). 0.09 (+/- 0.14), while in Tuanan the mean is 0.09 (+/- 0.14) (Figure 3.3.9). There was 11 days in Tuanan where over a quarter of long calls were responded to, while in Suaq that only occurred 3 times. A GLM returned a significant result for long call responses per long calls between the two sites (F=0.99 , p=<0.001) (Table 3.3.6).

3.40 Long Call Parameters

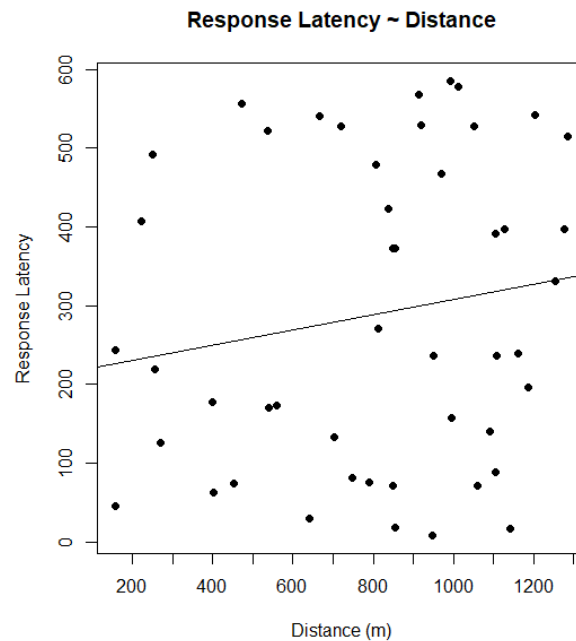*3.41 Response Latency, Distance & Pulse Rates*

Figure 3.4.0: Response latency plotted against distance of provoking long call.

A Kendall's rank correlation finds no relationship between the distance of a provoking long call and the latency of the long call response (tau = -0.009, p = 0.882) (Figure 3.4.0). Furthermore, there is no relationships between the latency of the response (tau = -0.061, p = 0.545), or the distance of the provoking call (tau = 0.026, p = 0.673) on the pulse rate of the long call response on a general, aggregate level (Appendix: 5.0.9, 5.1.0).
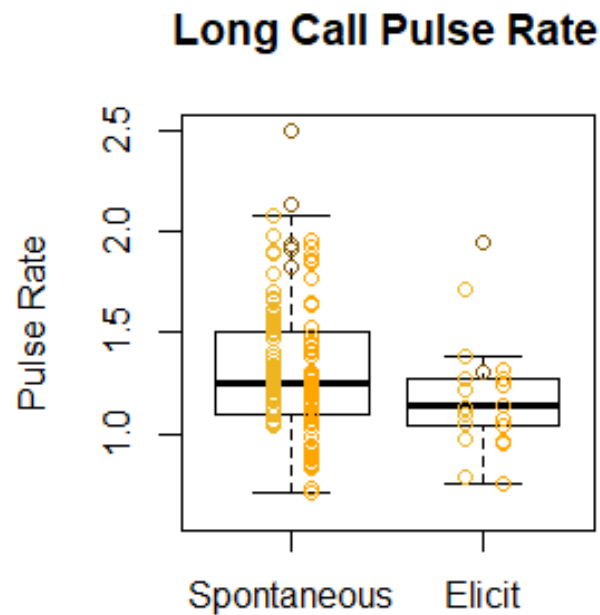
Long Call Pulse Rate

Figure 3.4.1: Mean pulse rate of long calls in spontaneous or elicited contexts. Different individuals are coloured in order (Islo, Balu, Xenix).

Table 3.4.0: GLM results for long call context predicted by pulse rate, with individual identity as a fixed effect.

Response	Effect	Effect type	Estimate	Std-Error	z Value	P Value	N Estimates	N Total
Long Call Context	(Intercept)	Fixed	0.23	1.43	0.267	0.790	2	192
Spontaneous/Elicit	Pulse Rate	Fixed	-1.78	1.10	-1.620	0.105	2	192

On an individual level, it appears as though long call context can not be predicted based on pulse rate alone. While elicited responses qualitatively seem to have faster pulse rates, the difference is not statistically significant (Table 3.4.0).

3.43 Long Call Durations

Mean long call length differs between these populations. Mean long call length in Suaq is 68.5 seconds (+/- 39.87) while long calls in Tuanan are comparatively shorter at 46.7 seconds (+/-22.45).

4.0 Discussion

4.10 Competition Systems & Long Calls

This thesis analyzed 2,196 long calls recorded at the Suaq, Sumatra and Tuanan, Borneo research sites to compare geographic variation in male-male competition behaviour. Flanged males in Tuanan and Suaq were found to operate under different mating and competition systems. Fruit availability drives males into the Tuanan research area, where calling male presence in Suaq does not seem to be affected by fruit availability. There are more flanged males roving through Tuanan on a yearly basis and more calling males are present daily in Tuanan compared to Suaq. This surplus of daily calling males explains the increase in long calls per km^2 seen in Tuanan, as there is no difference in individual males daily calling rates between the two sites. Flanged males in Tuanan respond to more of rival's long calls, as well as quicker than Suaq males.

The competitive landscape of Tuanan clearly differs from that in Suaq, males hear more long calls per day in Tuanan and are aware of the surplus of flanged male competitors. This also indicates a higher potential for flanged male eavesdroppers, and with the primary cost of long calls being in the social domain, an overall potentially higher cost for calling males in Tuanan compared to Suaq. Previous work has shown that males in Tuanan do get involved in more physical altercations than at Suaq (Dunkel, unpub.), and it does suggest that these confrontations are more necessary in Tuanan due to the unfamiliarity of these roving males and inherently more unstable dominance hierarchies (Spillmann et al., in prep.).

There appears to be a difference between the sites in how males use their long calls. While Suaq males show modest late-morning and pre-dusk calling peaks over the course of the day, Tuanan male calling behaviour is characterized by a sharp pre-dawn calling peak

with over 2x the calling rate at any other time of day. Van Schaik et al. (2013) showed that Suaq males plan their next day travel direction and announce that direction through long call direction before their night nest. It appears as though Tuanan males sort out who is where immediately upon waking, which is imperative knowledge for males in the area with increased competitors.

Higher calling rates correlate with higher response rates in Tuanan (Spillmann et al., in prep.) but do not in Suaq. It has been theorized that spontaneous long calls serve a different adaptive function through female attraction, compared to elicited long calls either as a response or to forest disturbance which serve a more male competition role (Spillmann et al., 2010). This could showcase the importance of female choice in Sumatra compared to Borneo. Studies that illustrate orangutan female choice through choosing to preferentially approach the long calls from the locally dominant male (Mitra Setia & van Schaik, 2007) and the earshot association suggested in Fox (2002) were found in Sumatran orangutans. It would then appear that Suaq males are more focused on utilizing their spontaneous long calls to attract females, rather than engaging in male-male competition through long call responses. While in Tuanan, calling males need to utilize both functions, because heightened call rates attract social attention, which further requires heightened response rates to defend their position in the dominance hierarchy.

The results showed that long call response latency does not change with distance of the provoking call on an aggregate level. If response latency measures emotional arousal, it does not appear as though closer long calls elicit a more emotional response. This could make sense if you consider that these males are already likely aware of one another's presence in the area, and closer long calls are not surprising, as they have already heard the other male announce their travel direction previously. On an aggregate level, long call response pulse rates do not show any relationship with the latency of the response, or the distance of the

provoking long call. While it could be expected that pulse rates on an aggregate level are heightened during long call responses with quicker response latencies, or from closer provoking long calls, no relationship is found. This suggests the role of the individual identity is paramount to not only assess an individual's emotional arousal due to long call context through establishment of a baseline. But additionally, the identity of the provoking caller could play a role in the differential arousal of the long call responder as well.

On an individual level pulse rate cannot differentiate between long call contexts in the Suaq data set. While the sample size for this Suaq analysis is comparatively small (3 individuals, 176 long calls), this can have two implications. First, is that pulse rate alone can not determine long call context, and other acoustic parameters must be considered. Second, is that there may be geographic variation in the differentiation of long call acoustic structure based on individual or environmental contexts. While Tuanan male long calls have been shown to differ acoustically through long call context (Spillmann et al., 2010), it may be possible that Suaq individual male's long calls are more acoustically homogenous. Either due to being less emotionally aroused during elicited calls, or to a relaxed necessity to differentiate between these contexts to potential female eavesdroppers.

4.20 Suaq & the 'Locally Dominant Male'

Behavioural data observations support a 'locally dominant male' mating system in Suaq. When long term data collection first started in the 90's at Suaq, one male, Arno was consistently able to mate guard and effectively monopolize Suaq females (van Schaik, pers. comm.) Since Suaq data collection resumed in 2007, again one male, Islo was consistently monopolizing female party time until 2014, when he appeared with a new, large facial wound. Islo was also the most consistently present flanged male in the study area during this time period. These males seemed capable of systematically excluding other males from mating opportunities under conditions where female monopolization potential was high. While Titan had seemed to be preferred by the females in 2014, he did not hold the position and there has not yet been a newly established locally dominant male with extended tenure in the Suaq research area.

Previous reports of a male takeover in another Western Sumatra field site, Ketambe (Utami Atmoko & Mitra Setia, 1995), saw the previous dominant male Jon quickly disappear and not be seen in the study area again. This situation at Suaq seemed to be a 'resisted takeover' where the previously dominant male Islo remained around the area, enjoyed another year in 2015 of preferential female association, and is still seen in the area recently. Another behaviour described in Utami Atmoko & Mitra Setia, (1995) was that of 'challenge calling' where the challenging, newly flanging male has extremely high call rates within the area, with seemingly no external circumstances provoking these calls. This behaviour is seen in the Suaq ALS data set in the outliers of long calls per calling male and was personally observed during my own field season. One of these 'challenge calling' males, Xenix certainly fits the described role of a challenging male, by being an impressively large, unflanged male who has frequently been seen in the research area in past study years and had now only begun

to flange now in periods of instability. The other male displaying this behaviour is the previously locally dominant male Islo. They both had several days of heightened call rates, and after reviewing the ALS data, there was no other calling male in the study area.

The absence of this heightened, 'confrontational assessment' model of male-male competition in Suaq is interesting considering the current lack of a locally dominant male. Becoming the next locally dominant male would secure future paternity concentration which means the potential payoff and highest benefit of an increase in competitive behaviour would be currently. While we have referred to this time in Suaq as 'instable', there doesn't seem to be a rise in confrontation behaviour, or long call response behaviour that would match the consistent instability of dominance hierarchies found in Tuanan. One contributing factor could be male familiarity, as there is a lack of new, unfamiliar males roving through the Suaq research area, compared to Tuanan. Although the locally dominant male is absent, they still know where they stand in the hierarchy is relation to the other Suaq males, and thus do not require frequent confrontation. These 'challenge calling' behaviour and absence of a rise in confrontation through long call responses could again be demonstrating the role of female choice in becoming the locally dominant male, through the female attraction function of spontaneous long calls. It does seem that the Suaq male dominance hierarchies are inherently more stable than the Tuanan hierarchies, even in the absence of a locally dominant male.

4.30 Island Ecology & Orangutan Evolution

One of the key elements driving geographic variation in orangutans is due to fruit availability. The fertile volcanic soil in Western Sumatra and subsequently higher fruit availability than Borneo (Marshall et al., 2009; Wich et al., 2011), can account for some of the differences seen in gregariousness or sociability. However, the results of my models did not change when controlling for fruit availability. This could indicate that these differences in competition behaviour are rooted deeper beyond ecosystem productivity and could be a result of separate evolutionary trajectories from the ~3 million years of separation (Nater et al., 2017). However, it is important to keep in mind that the Suaq data covers a smaller, higher range of fruit availability (11.35 – 14.43) and there could be an influence of fruit availability on male ranging at lower FAI levels. These island differences in forest productivity and fruit availability would of course facilitate and influence each species respective evolutionary path, but immediate habitat productivity alone does not seem to explain this difference in competitive behaviour.

The higher fruit availability in Sumatra supports higher population densities and allows females to be comparably more social in Sumatra than Borneo (Wich et al., 1999). This could influence and increase the female monopolization potential for any one flanged male. A locally dominant male could then also obtain a sufficiently nutritious diet over a smaller total ranging area. There seems to be evidence that suggests that the ancestral mating system state in orangutans resembles a more uni-male harem-style social organization unit, with the change towards a more semi-solitary lifestyle occurring ~5 million years ago due to increased food stress (Harrison & Chivers, 2007). If that is the case these fertile forests in Sumatra, and the 'locally dominant male' mating system likely closer represent the ancestral condition in orangutan evolution, compared to the more derived 'promiscuous, roving male'

mating system found in Borneo. The further fruit inconsistency and scarcity found in Borneo as these orangutans travelled further east could then only exacerbate this departure from the ancestral state and make it near impossible for female monopolization to occur. Not only would a larger home range be necessary to ensure a flanged male obtains his daily caloric needs, but these less productive forests would also support lower female population densities. Thus, the promotion of the 'promiscuous roving male' mating system, with a confrontational assessment approach of competition and reduced unflanged male reproductive advantage.

4.40 Competition Differences in Populations or Species?

In order to assess the generalizability of these results as to whether these competitive differences are a result of population or species level differences, there are two considerations. First is to consider how disturbed these populations are, and whether they represent how these orangutans would behave without anthropomorphic influence. Second is to assess whether these sites are representative of other populations of their species or subspecies.

The anthropomorphic influence on current orangutan distribution is undeniable. Recent estimates of remaining orangutan population sizes including 15,000 for Sumatra (*Pongo abelii*) (Wich et al., 2016), 70,000 – 100,000 for Bornean (*Pongo pygmaeus*) (Voigt et al., 2018), and only 800 individuals for the newly described *Pongo tapanuliensis* (Nater et al., 2017). Current populations are limited to isolated forests in Borneo and Sumatra, with all populations being endangered (Zhi et al., 1996; Nater et al., 2011). These numbers can be directly attributed to many human activities such as clear-cutting forests for mines, farmland or palm oil plantations, illegal loggers who can selectively change forest canopy composition and homogony, direct hunting due to orangutan encroachment on farmlands or less commonly bushmeat, or capture for the illegal pet trade.

While Bornean orangutan population estimates are declining rapidly (Voigt et al., 2018), in contrast local populations in Tuanan seem to be relatively higher than other study sites within Borneo (van Schaik et al., 2005), and possibly continuing to increase. One such influx of new individuals can be explained by forest fires in adjacent forests (Meric de Bellefon, 2017). Another explanation could be due to Camp Rilis, an orangutan release site that was active in 2006-08 roughly 10 kilometres away from the Tuanan research area. Given the male bias towards dispersal in orangutans, and 10 kilometres being suggested as a

possible dispersing distance for males (Buckley, 2014) this could additionally be driving this abundance of males in the Tuanan research area.

Suaq is also not immune to an increased pressure in the study area, forest area to the south of the study grid has recently been cleared and could be driving this prolonged period of instability in the male dominance hierarchy, as well as new mother offspring pairs seen in the area. Additionally, Lank Bangko has sporadically served as an orangutan re-location site roughly 5 kilometres from the Suaq research area. It appears both sites are subject to various amounts of human influence and it's becoming unlikely these two sites represent truly wild populations of orangutans. However, this does not mean that it isn't possible to assess geographic variation from these study sites.

Analysis of paternity skews at orangutan research sites provide a great measurement for the outcome of male-male competition and post-hoc analysis of competition system present. Studies at Ketambe (Utami-Atmoko & Wich, 2002) as well as Suaq (Lenzi, 2014) show a high paternity skew, which is in line with expectations of a 'locally dominant male' model, and stable dominance hierarchies. Low skew outcomes of paternity are found in Borneo at Kinabatangan (Goossens et al., 2006) which align with 'promiscuous roving male' expectations. However, it does seem that brief periods of concentrated paternity from an individual male are found in Tuanan (van Noordwijk, unpub.) and Kabili Sepilok (Tajima et al., 2018) but none show multiple years of extended paternity concentration or female preference seen in Sumatra. These studies would then support that the measured competition differences shown in this thesis may be more broadly applicable to island differences in competition, rather than just local population differences.

4.50 Study Reflections

The extensive potential of the acoustic localization system to study flanged male orangutan calling behaviour is obvious. It offers an unbiased view into individual male orangutan long call interactions, study area presence, as well as emotional arousal with sufficient sample sizes. However, traditional behavioural data collection through focal animal follows are still just as necessary, to record behavioural states, conspecific associations, physical confrontations, as well as validate these data procedures. Thus, the best usage of this ALS is to supplement ongoing research, rather than replace. With further streamlining of data management techniques, I can imagine these methods could be replicated with potentially smaller costs and quicker data turnaround. While this thesis captured a small glimpse of Suaq flanged male long call behaviour in space and time, lengthened temporal analysis can further elucidate flanged male presence and long call behaviour. To my knowledge, this ALS project represents the largest sample size recorded of orangutan long calls, and a data set with enormous potential for further research questions to be answered.

4.60 Future Directions

The role of the individual remains paramount in analyzing individual long call behaviour and interactions. Usage of an automated caller recognition algorithm such as in Spillmann et al. (2016) can greatly increase the resolution of this data set and allow questions of finer detail to be answered. Analysis of additional long call acoustic parameters could answer further questions about emotional arousal and the meaning of long call contexts in Sumatran orangutans. Individual flanged male ranging responses to long calls could also be investigated due to the localization aspect of this ALS to capture all flanged male avoidance behaviour and implications for dominance hierarchies. ALS data can supplement focal follow data to analyze long call ranging responses of all age-sexes to test the adaptive functions of Sumatran or Bornean flanged male long calls. Temporal studies of long call behaviour would serve to elucidate questions in orangutan male careers. Temporal changes in Suaq could particularly showcase how a locally dominant male changes in their long call and response rate behaviour throughout the pre-, peri-, and post- eras of their locally dominant tenure. Calling species with individually identifiable calls are great candidates for this methodology to study calling behaviour in detail or map out home range estimates where long term behavioural data is missing. Ongoing conservation efforts could additionally benefit through calling species surveys to estimate population densities or ecosystem diversity, or for continued monitoring of protected areas. Passive acoustic data collection techniques such as the ALS offer an unbiased view into calling behaviour and has been used in this study to map out flanged male long call behaviour in detail not yet recorded.

4.70 Conclusions

Ultimately, detailed analysis of flanged male orangutan long calls revealed innate geographic variation in male-male competition behaviour. There are less roving males coming through the Suaq research area, and this increase in male familiarity leads to more stable dominance hierarchies. Overall, there are less flanged male competitors in the Suaq forests. The competitive landscape in Suaq seems to be more relaxed, with less long calls occurring, and less long calls being responded to, at slower response latencies compared to Tuanan. Tuanan males daily calling behaviour is characterized by a pronounced pre-dawn calling peak, not found in Suaq. Calling males in Suaq are not necessarily responding more, as seen in Tuanan and physical confrontations are infrequent between Suaq males. In Tuanan a 'confrontational assessment' approach is found in male-male competition where flanged males continually assess other males through individual identity, which leads to frequent confrontations for males unfamiliar with one another or displaying high competition motivation (Spillmann et al., 2017). However, the flanged males in Suaq compete through 'systematic exclusion', where the more stable dominance hierarchies leads to the highest ranking 'locally dominant male' excluded rivals from mating opportunities.

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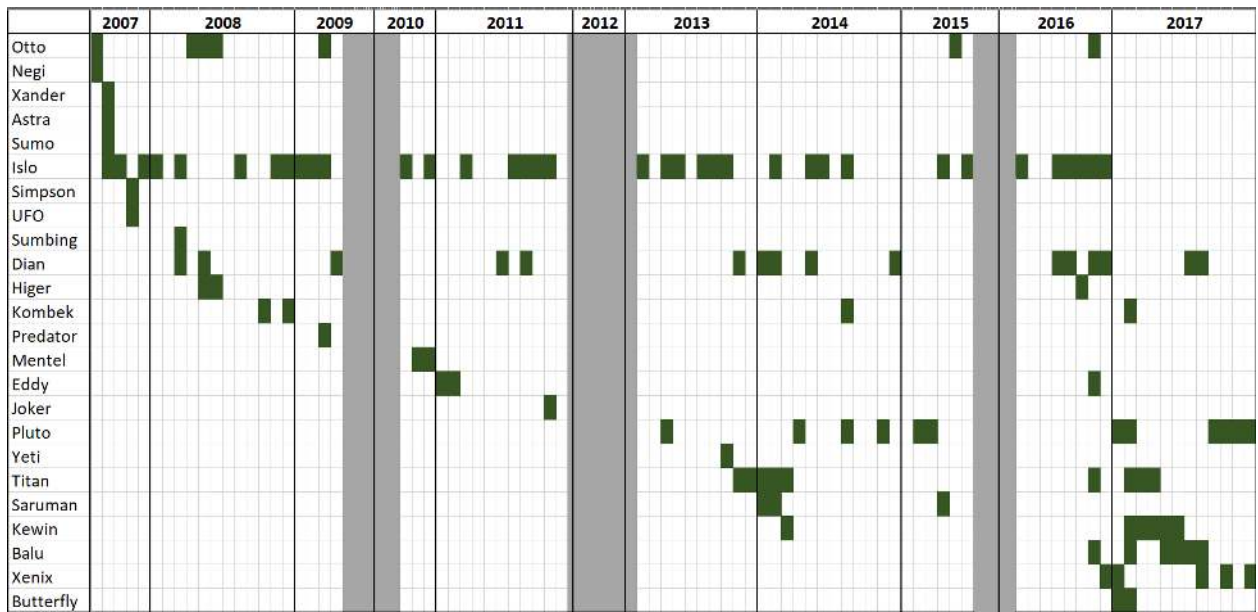
5.0 Appendix

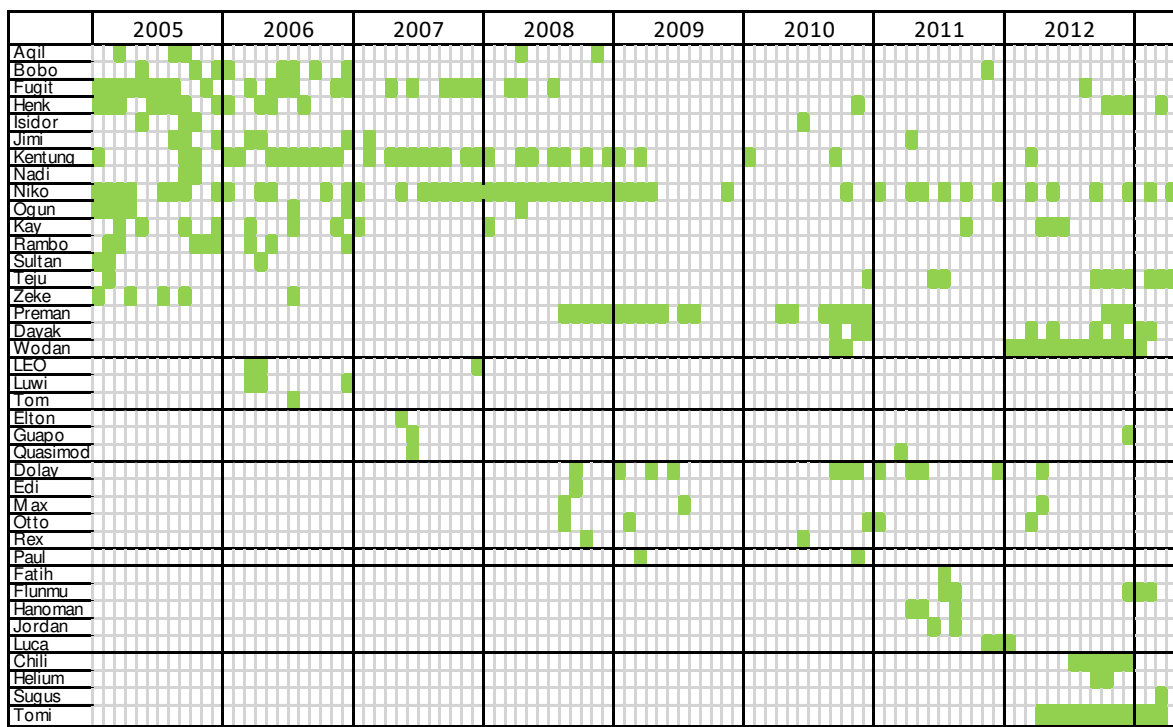**Figure 5.0.1:** Flanged male monthly presence in Suaq.

Figure 5.0.2: Flanged male monthly presence in Tuanan.
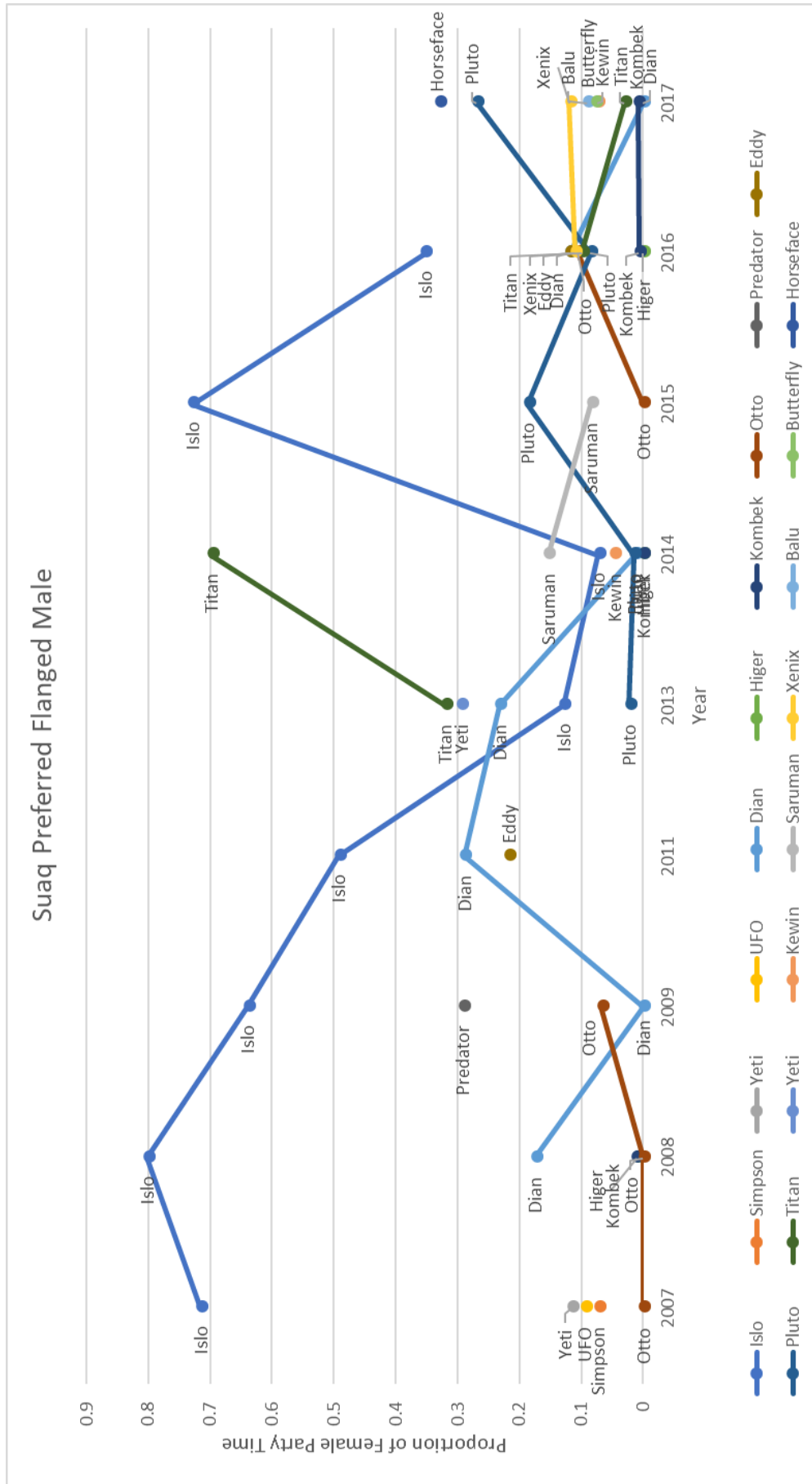
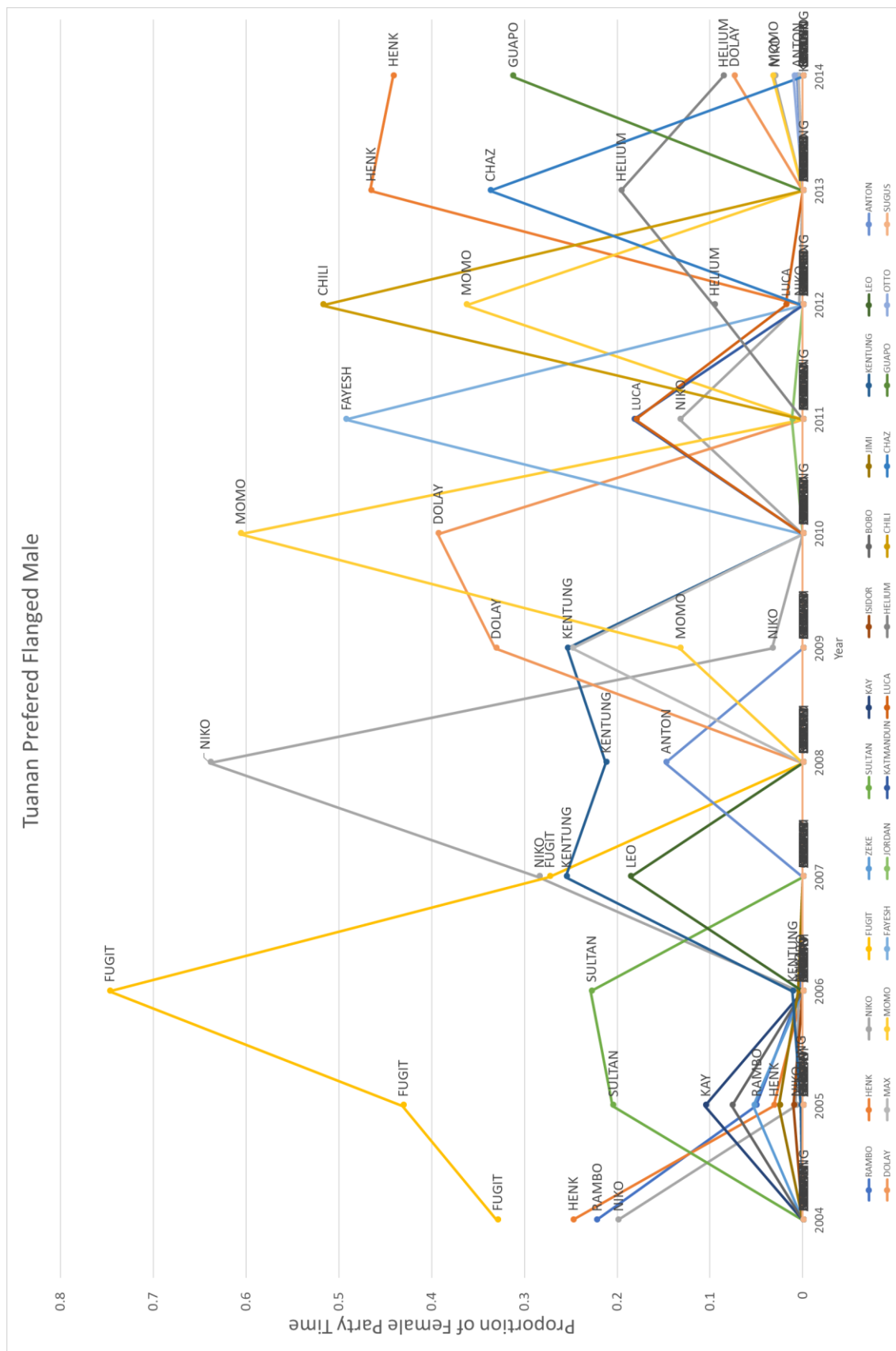**Figure 5.0.3:** Flanged male proportion of female party time by year in Suaq.

Figure 5.0.4: Flanged male proportion of female party time by year in Tuanan.
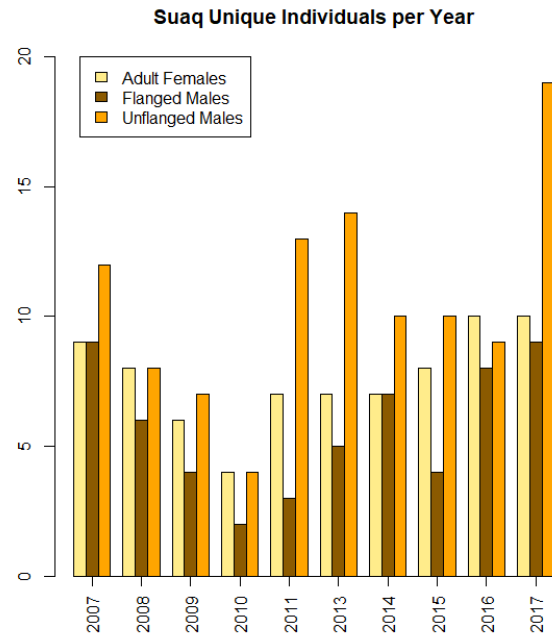
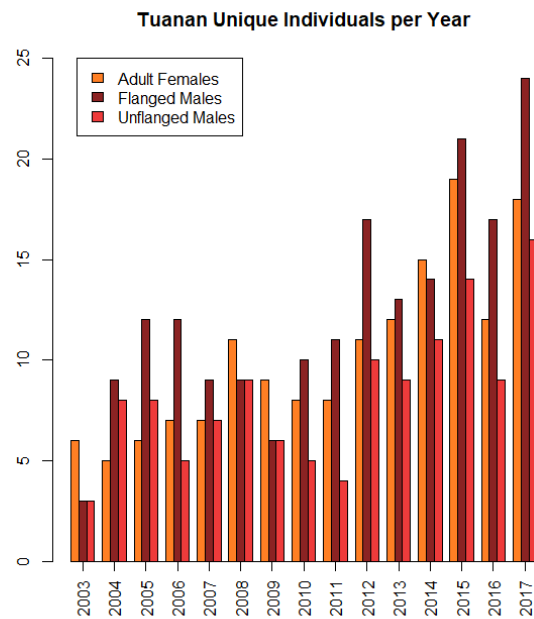**Figure 5.0.5:** Unique individuals per year, separated by age-sex class in Suaq.

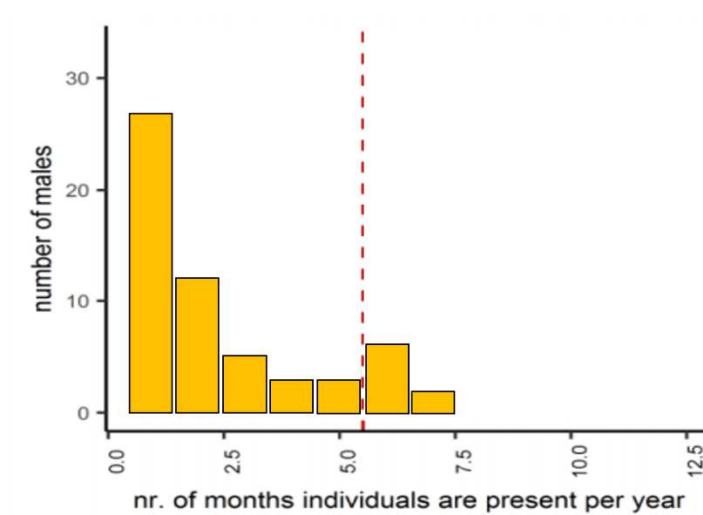**Figure 5.0.6:** Unique individuals per year, separated by age-sex class in Tuanan.

Figure 5.0.7: Number of months present per individual male per year in Suaq.
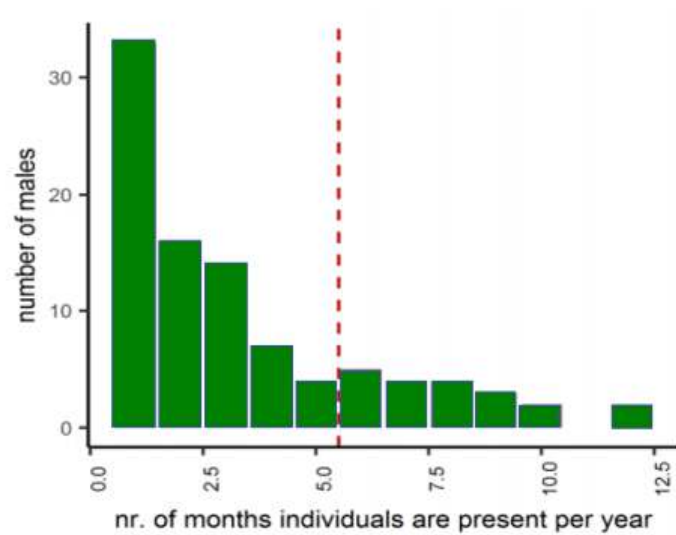

Figure 5.0.8: Number of months present per individual male per year in Tuanan.
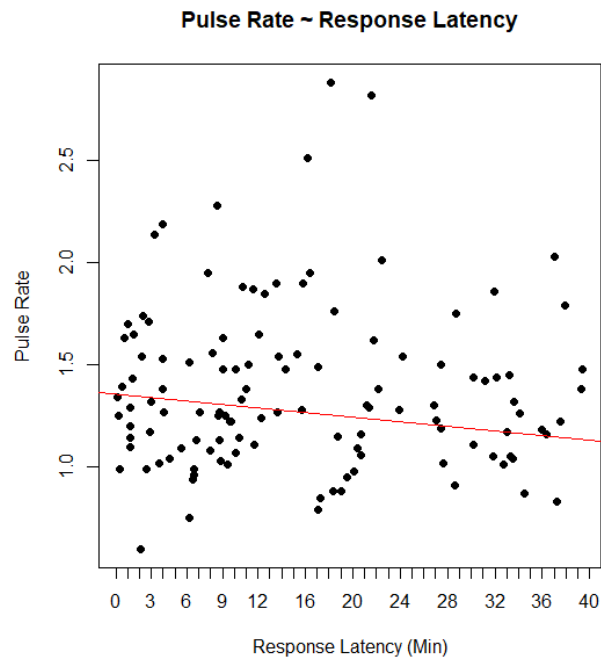
Figure 5.0.9: Pulse rate plotted against long call response latency.
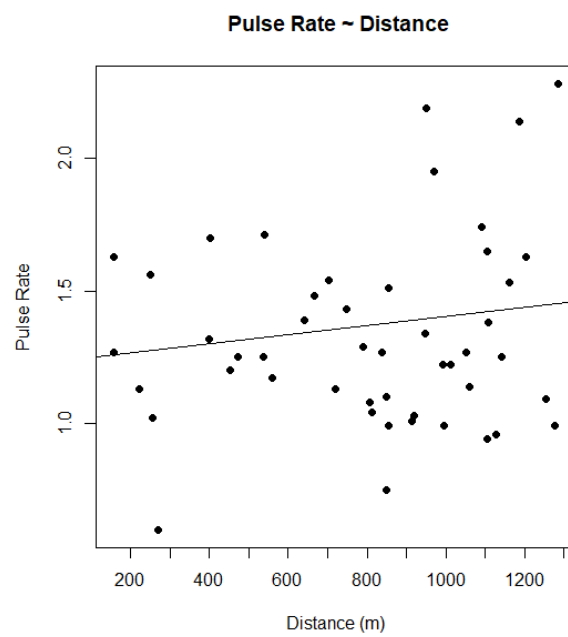
Figure 5.1.0: Pulse rate plotted against elicited response distance.

Table 5.1.1: Cohen's kappa IOR test calculation.

	Yes	No	**Total**
Yes	232	54	**286**
No	6	18,968	**18,974**
Total	**238**	**19,037**	**19,260**

Table 5.1.2: Index of concordance IOR test, divided by estimated long call distance from the microphone.

	Agree	Disagree	Total	IC%
Close	81	9	90	90
Med	86	5	91	95
Far	65	46	111	59
Total	**232**	**60**	**292**	**79**

Long Call Extraction IOR

An inter-observer reliability (IOR) test was calculated to ensure data consistency during the extraction process and that long call recognition was similar between two different observers. A total of 6 recorders, each with 3 weeks of continuous recording were used for this IOR.. A cohen's kappa value was calculated to check for both negative and positive agreement of behaviour. This k value was 0.989 indicating a very high level of agreement. This figure might not be a perfect indicator of overall agreeance, due to 18,968 false positives from the recognition algorithm that were easy to discard as long calls. Thus, an overall index of concordance was also calculated. This percentage is 79%, which would not be acceptable for data sharing, however closer inspection of these agreeance and disagreement proved otherwise (Table 5.0.2). Long calls from an estimated 'close' and 'medium' distance of the recorder was agreed upon at 90% and 95% respectively. Overall agreement of 79% was primarily being driven by only 59% of long calls being agreed upon from an estimated 'far' distance from the recorder. This is less problematic than it seems, because if these long calls originated from inside the ALS grid, they would be found at recorders closer to the long call origin. If these long calls originated from outside the ALS grid, localization and identification are not possible, and the possible analysis is limited.
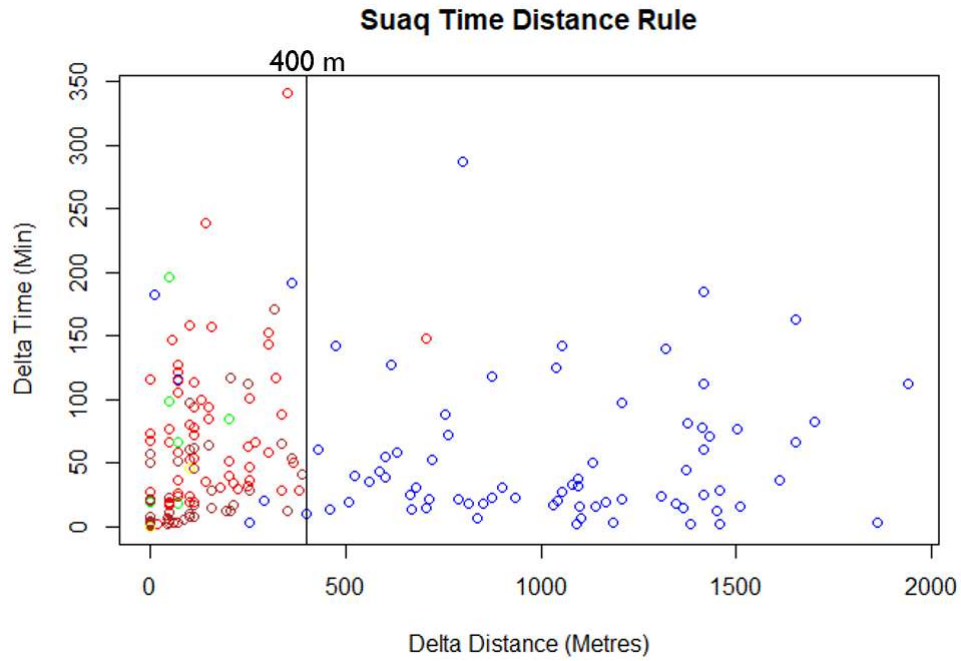
Figure 5.1.3: Figure of long calls used for establishment of the time distance rule.

Suaq Time Distance Rule

    Long calls were plotted from focal follow days at 0,0. Subsequent long calls were plotted with their difference in time and distance, blue indicates a long call heard, while the colours represent an individual's second long call of the day. That second long call then becomes the next 0,0 plot and further long calls heard are again plotted. The distance of 400 metres was chosen to limit the amount of false positives (4/216) and negatives (1/216) it would generate.

Table 5.1.4: Yearly follows >5 hours, unique males and silent long call activity in Suaq.

	2007	2008	2009	2010	2011	2013	2014	2015	2016	2017	Total
Total 5hr Follows	15	24	5	4	20	8	19	14	27	63	199
Unique Males	1	4	3	2	3	3	6	4	5	6	37
Silent Follows	4	13	3	2	1	4	11	8	13	11	70
Silent Males	0	2	2	1	0	1	1	0	2	0	9
Silent Follows Proportion	0.27	0.54	0.60	0.50	0.05	0.50	0.58	0.57	0.48	0.17	0.35
Silent Males Proportion	0.00	0.50	0.67	0.50	0.00	0.33	0.17	0.00	0.40	0.00	0.24

Table 5.1.5: Yearly follows >5 hours, unique males and silent long call activity in Tuanan.

	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	Total
Total 5hr Follows	3	19	122	93	63	70	87	70	46	154	100	156	195	217	157	1552
Unique Males	1	5	11	10	4	6	7	9	13	15	13	16	21	17	17	165
Silent Follows	0	9	70	38	27	26	39	37	27	26	25	48	99	133	58	662
Silent Males	0	1	2	1	0	0	1	3	6	3	2	2	6	5	4	36
Silent Follows Proportion	0.00	0.47	0.57	0.41	0.43	0.37	0.45	0.53	0.59	0.17	0.25	0.31	0.51	0.61	0.37	0.43
Silent Males Proportion	0.00	0.20	0.18	0.10	0.00	0.00	0.14	0.33	0.46	0.20	0.15	0.13	0.29	0.29	0.24	0.22