

**Acoustic characteristics of long calls produced by male orang-utans (*Pongo pygmaeus wurmbii*) advertise individual identity, context and subsequent direction of travel.**

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**Abstract**

Flanged male Bornean orang-utans (*Pongo pygmaeus wurmbii*) produce long distance vocalisations or long calls that can be heard over a kilometre away. If a receiver can identify the caller and perhaps even obtain information about their dominance rank, then they can choose to approach or avoid the male depending on their own sex, quality and needs. Long calls are produced under a number of circumstances; if information about the caller is transmitted in the call then perhaps so is information relevant to the context. Anecdotal evidence suggests the orang-utans call indicates their future direction of travel. In this study acoustic analysis of the long calls produced by the orang-utans at Sabangau, Central Kalimantan shows individual discrimination between the males and discrimination between the calls made under the different contexts wild orang-utans encounter. Additionally this study demonstrates, for the first time, experimental evidence for orang-utans advertising their intended travel route by long calling and then continuing in the direction of the call. This behaviour in turn provides evidence for orang-utans using their long call to spatially orient themselves and perhaps even to co-ordinate a network of loose associations. However there are a number of possible functions for the long call and the discrimination between contexts suggest that it may even differ under different contexts.

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## 1 Introduction

Amongst non-human primates, especially those in low visibility environments, long distance vocalisations, known as loud or long calls, are widespread (see review by Delgado, 2006). Acoustic analysis of these long calls has shown evidence for individual variation across a number of primate species (e.g. Marler & Hobbet, 1975; Waser, 1977; Wich et al., 2003; Sabatini & Ruiz-Miranda, 2008; Price et al., 2009), including those produced by the Bornean orang-utan, *Pongo pygmaeus wurmbii* (Delgado, 2003; Spillmann et al., 2010).

Adult orang-utans do not typically associate with one another, living a semi-solitary lifestyle due to feeding competition and the energetic costs of association (van Schaik & van Hoof, 1996; Delgado, 2003; Harrison et al., 2010). However there is evidence for social structure, including preferential associations amongst adult females (MacKinnon, 1974; Rijksen, 1978; Galdikas, 1985; Delgado, 2003) and between sexually available females and dominant males (van Schaik & van Hoof, 1996; Delgado, 2003; Harrison, 2010).. Given the highly dispersed nature of adults, it seems likely that some form of communication is being utilised to establish and maintain spatial co-ordination. Long calls may provide a mechanism through which associations between individuals within a dispersed community are co-ordinated, including in mating contexts (MacKinnon, 1974; Delgado & van Schaik, 2000; Delgado, 2003).

Amongst orang-utans, long calls are sex and age specific with only adult flanged males able to produce them. They represent one of the most frequent vocalisations produced by the species and can carry over a kilometre in optimal weather conditions and over flat terrain (Galdikas, 1983; Mitani, 1985b). They have a typical duration of 1 to 2 minutes consisting of 3 distinct stages (Fig.3). Calls begin with a series of repeated, low frequency, low amplitude “grumbles”; a series of higher amplitude, higher frequency pulses are interjected and the call then slows down

and concludes with a series of low frequency, low amplitude “bubbles” (Galdikas 1983; Mitani, 1985a; Delgado, 2003).

At a number of sites in Sumatra and some in Borneo acoustic analysis of the calls has found them to be individually recognisable, furthermore a mixture of playback and behavioural observations also show the receiver to recognise the calls of an individual orang-utan and respond accordingly (Mitani, 1985a; Utami & Mitra Setia, 1995; Delgado, 2003; Lameira & Wich, 2008). Based on the assumption that individuals are individually identifiable from their calls, a number of hypotheses have been proposed as to the exact function of long calling. The most established of these is the spacing of males based on relative rank, whereby subordinates will actively avoid dominant callers, but dominants will approach subordinate callers, indicating that individual recognition is taking place (Galdikas, 1978; Galdikas, 1983; Mitani, 1985b, 1990; Delgado, 2010; Morrogh-Bernard, In Prep). Another highly regarded, but less experimentally consistent hypothesis is that the calls function to attract cycling females and thereby facilitate mating (Mitani, 1985b; Utami & Mitra Setia, 1995; Delgado, 2010).

In their recent study Spillmann et al. (2010) concluded that orang-utans in Tuanan, a similar site to that used in this study, produced different long calls in different contexts. If this is indeed the case, it seems likely that the long calls produced under different contexts have different functions and that this could be further manifested through the orang-utan’s behaviour after producing a call under a given context.

Consistent with both hypotheses is the theory that males call in their direction of travel and therefore announce their arrival in an area, potentially both to attract females and to warn competing conspecifics of their future movement. Anecdotal evidence from van’t Land (1990), van Schaik (1996) and Damerius & van Schaik (2007) suggests that this is indeed the case and that, on days when they produced more long calls males would travel in a straighter direction.

However, until now this anecdotal evidence has not been published.

In this study, I first examined the acoustic characteristics of long calls made by flanged male orang-utans to see if they reflect individuality, I then re-examined Spillmann et al.'s (2010) conclusion that males produce acoustically different calls in different contexts. I then examined the direction of the long call and the direction travelled between calls to see if the direction of the call indicated the direction of travel. Finally I included context as an interactive variable with direction of call to assess if any relationship between the direction of the call and the direction the individual travelled varied with context.

For any of the proposed functions to be feasible it is fundamental that receivers can identify the caller, therefore individual discrimination of long call characteristics has to be examined in any pilot study. To fully understand the function of long calls in orang-utans, it is important to determine whether the acoustic structure of a long call changes according to which behavioural context it was made under, as this will provide potential evidence for differing functions under each context or if the null hypothesis cannot be rejected then there is also the possibility of just one function. This study is especially significant as, to date, no experimental study has analysed the long calls made by the orang-utans at Sabangau.

I expected to find that the acoustic characteristics would reveal both the caller's identity and reflect the context under which the call was made. I expected to find that direction of the call would indicate the orang-utan's subsequent direction of travel and that this relationship would be more significant when calls were made spontaneously than in any other context.

## **2 Methods**

### **2.1 Study site**

Data were collected in September 2007, September 2009 and between June-September 2010 within the Sabangau National Park, Central Kalimantan, Indonesia. The National Park covers 568 000 hectares of ombrogenous mixed peat-swamp forest between the Sabangau and Katingan Rivers. The study area itself was located in the 500km<sup>2</sup> Natural Laboratory for the Study of Peat-swamp Forest (Laboratorium Alam Hutan Gambut, LAHG), situated in the North of the park (2°19' S and 113°54' E).

Sabangau holds the largest contiguous population of Bornean orang-utans existing today, estimated at 6,900 individuals (Morrogh-Bernard *et al.*, 2003; Harrison *et al.*, 2010) Sabangau remains unfragmented, but was selectively logged from 1973 to 2005 (illegally so from 1997 onwards). There are five distinct habitat sub-types identified in the Sabangau, varying in floristic structure and composition (Harrison *et al.*, 2010). This study was conducted in the largest of these habitat types, the mixed-swamp forest, which supports the bulk of the orang-utan population (Morrogh-Bernard *et al.*, 2003). All research was carried out as a part of, and with the express consent of, the OuTrop-CIMTROP multidisciplinary research project.

### **2.2 Long call recordings**

Long calls were recorded during focal follows of three flanged males (Jupiter, Peter Pan and Salvador). Once encountered, animals were followed from night nest to night nest until lost, abandoned (after a maximum period of 10 consecutive full day follows) or the animal left the study area. Recordings were made opportunistically using a Marantz TATE PMD620 Digital recorder (Marantz Corporation, Kenagawa, Japan) (Sampling rate was set to 44100 Hz and

sample size to 16-bit PCM) and a Sennheiser ME-66 shotgun microphone (Sennheiser Electronics, Wedemark-Wennebostel, Germany) or an Audio-Technica AT897 shotgun microphone (Audio-Technica Corporation, Tokyo, Japan). Each time the orang-utan called, regardless of whether the call was recorded, the time, the call's direction, estimated using a compass, and the behaviour immediately before and after the call were noted. The behavioural notations included the initial direction of travel, taken from a compass bearing, once the call was complete.

The behavioural context under which the call was made was also recorded. The contexts were divided into:

- i) Spontaneous – calls made with no disturbance
- ii) Long calls accompanied by snag crashing
- iii) Long calls in response to a tree fall or another males long call
- iv) Long calls made with a female/females in attendance (Table. 1).

(For some of the long calls behavioural context was not recorded, these calls were used only to assess individuality and direction of travel.)

### **2.3 Acoustic Analysis**

The long call recordings were transformed into spectrograms (window type = default, window size = 1024 samples, bandwidth = 61.9Hz, time-grid spacing = 102 samples, frame overlap = 90%, frequency grid spacing = 43.1Hz) using Raven Lite. 1.0 (Update 18, Copyright 2009, Cornell Lab of Ornithology Bioacoustics Research Program). This was achieved by converting waveforms into spectrograms by fast Fourier transformation. A number of frequency and

temporal variables were measured using the software (Table 2.).

To produce descriptive variables pulses were classified according to Spillmann et al.'s (2010) modification of Ross & Geissmann's (2007) system for ascribing pulse type. The system describes 5 pulse types: Roar (high amplitude, see below); Huitus (high amplitude, steeply ascending & descending parts that are unconnected); Intermediary (low amplitude, rises & falls then rises & falls again); Sigh (low amplitude, short rise connected to a long fall); and Bubbles (low amplitude, looks like a cracked sigh). Spillmann et al.'s (2010) modification is to reclassify pulse type Roar into three subgroups: volcano (sharp tip, high frequency), roar (more rounded, low frequency) and low roar (half the frequency of the other subgroups) (Fig. 3).

While Spillmann et al. (2010) used only one pulse type (roar), a number of previous analyses have used all high amplitude pulses occurring in the first 30 seconds of the call. Therefore for my analyses I have used the latter method, allowing for greater comparison with previous results and analyses a greater range of acoustic characteristics.



Table 1. Overview of the all long calls encountered and contexts they occurred in.

| Focal Individual  | Spontaneous   | Accompanied by snag crash | Response to snag crash or call | With female present | Unknown  | <b>Total (NR)</b> |
|-------------------|---------------|---------------------------|--------------------------------|---------------------|----------|-------------------|
| Peter Pan         | 18 (5)        | 3 (1)                     | 3 (1)                          | 17 (6)              | 0        | <b>41 (13)</b>    |
| Jupiter           | 10            | 1                         | 3 (1)                          | 0                   | 4        | <b>18 (1)</b>     |
| Salvador          | 16 (4)        | 3                         | 1                              | 0                   | 0        | <b>20 (4)</b>     |
| <b>Total (NR)</b> | <b>48 (9)</b> | <b>7 (1)</b>              | <b>7 (2)</b>                   | <b>17 (6)</b>       | <b>4</b> | <b>79 (18)</b>    |

(N.B. NR indicates how many of calls not recorded or poor quality that are included in the analysis of subsequent travel direction, additionally 6 calls, 4 spontaneous, 1 snag, 1 with female, were not included in the directional analysis as no movement occurred after their being made)

Fig. 1. Spectrograms of partial long calls from Salvador (above) and Jupiter illustrating the different pulse types used in analysis.

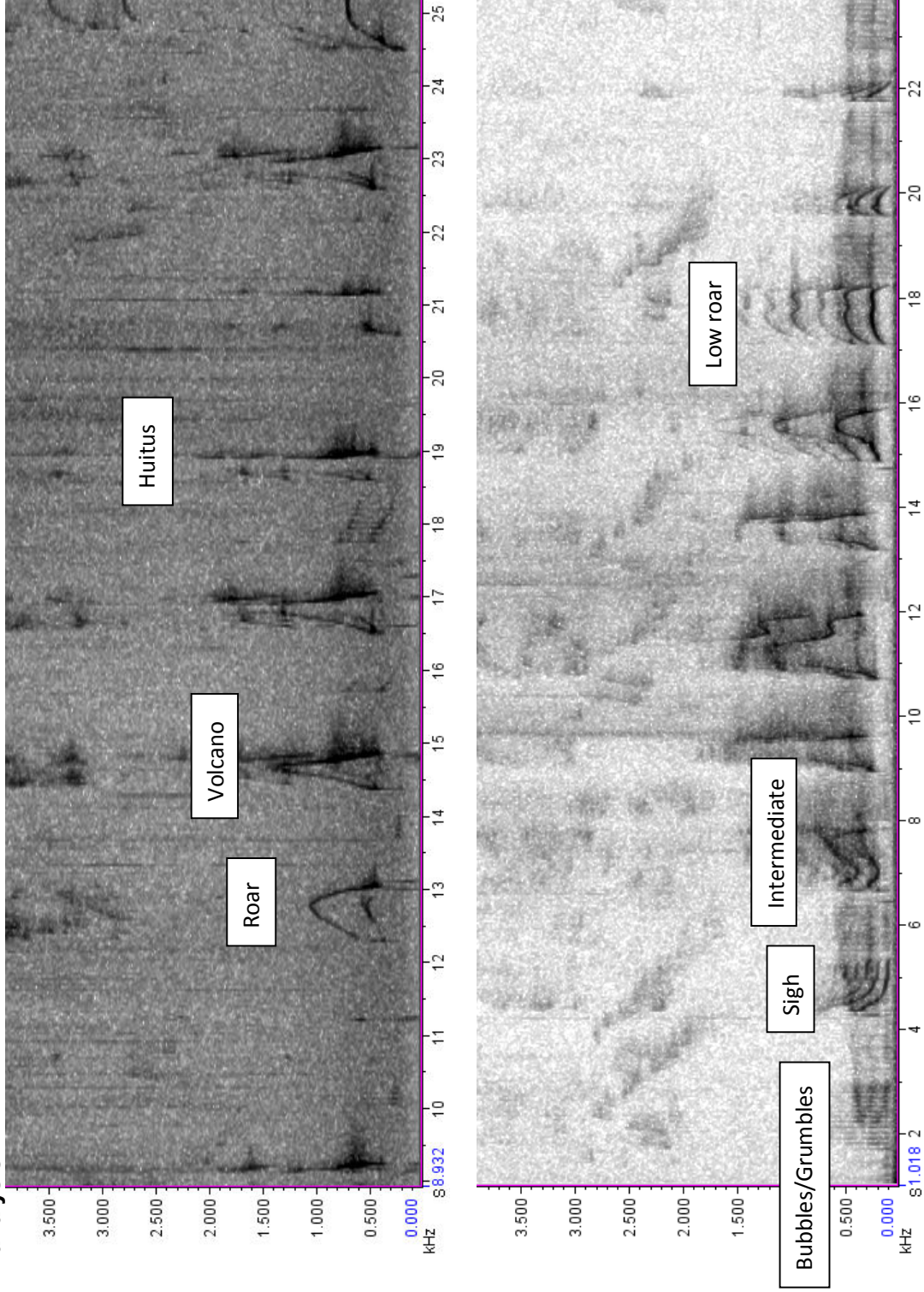


Table 2. Overview of variables measured in Raven Lite, derived variables and descriptive variables.

| Measures from Raven for each pulse | Unit | Descriptive variables       | Unit      |
|------------------------------------|------|-----------------------------|-----------|
| F0 start                           | Hz   | Duration of call            | s         |
| F0 high                            | Hz   | Pulses                      | #         |
| F0 end                             | Hz   | Roars                       | #         |
| F0 rising duration                 | s    | Volcanoes                   | #         |
| F0 rising range                    | Hz   | Huitus                      | #         |
| F0 falling duration                | s    | Low roars                   | #         |
| F0 falling range                   | Hz   | Intermediates               | #         |
| Duration of pulse                  | s    | Sighs                       | #         |
| Duration of interval               | s    | Bubbles/grumbles            | # of sets |
| <b>Derived variables</b>           |      | Call rate*                  | #/s       |
| Rising slope                       | Hz/s | Call rate during first 30s* | #/s       |
| Falling slope                      | Hz/s |                             |           |

(\*not including bubbles/grumbles)

## **2.4 Travelling data**

For ranging data, to be used in other studies, a GPS point was taken every 30 minutes using a Garmin GPSmap 60Cx, GPS unit (Garmin, Olathe, Kansas, USA). From this the actual direction of the orang-utans movement between calls, or until construction of a night nest was calculated (Fig. 4). Alternatively for the pre -2010 data, the direction between calls was calculated using the cumulative compass bearings and distances estimated as part of the behavioural observations.

## **2.5 Additional observations**

Alongside collecting recordings from the focal individual in Sabangau Forest National Park additional ethological and feeding ecology variables were recorded ad libitum for use in a number of other studies.

## **2.6 Statistical analysis**

### **2.6.1 Individuality and context**

Discriminant function analysis was carried out using SPSS 18.0 (SPSS Inv., Chicago, USA) to determine possible identification of the males by the acoustic characteristics of their long calls and the identification of which context the call was produced under. The analysis was initially undertaken entering the factors in a stepwise procedure to reduce the number of variables. The analysis was then run with Peter Pan and Jupiter's data split into 2010 vs. 2009 and 2010 vs. 2007 respectively, this was to see what changes if any had occurred in the intervening years as the data set was not continuous.

To analyse the discriminant functions of context, firstly all contexts were classified as spontaneous, with snag crash, response and with a female present and subjected to a stepwise analysis. In the second analysis the contexts were grouped according to arousal level, as with Spillmann et al.'s study (2010), where snag crash and response were included as one group to indicate an aroused state, again the analysis was stepwise.

### **2.6.2 Call direction, subsequent travel direction & context**

To analyse the potential relationship between call direction and initial direction of travel or overall direction of travel linear regressions were used between first call direction and initial direction of travel, and secondly call direction and overall direction of travel. The linear regressions were then repeated using the variables obtained under each specific context.

## **3 Results**

### **3.1 Individuality**

Individual discrimination of the orang-utans with all data included was possible for 96.9% of cases, with all variables being input with a stepwise methodology. 6 variables were found to be highly significant factors according to wilks-lambda test (see 3.3, table 3 and chart 1)

When Jupiter's data was split into '07 and '10, and Peter Pan into '09, '10, with Salvador remaining the same individual discrimination was possible for 93.8% of cases, with all variables input stepwise. 8 variables were found to be highly significant factors (See 3.3 & table 3).

### **3.2 Context**

Discrimination of all contexts was possible for 65.2% of cases with all variables input in a stepwise procedure. Only one variable, no. Of volcanoes was significant. (See table 3 & 3.3)

When the two aroused conditions were combined the discrimination of contexts increased to 78.3% of cases, with 4 variables found to be highly significant factors. (See table 3 & 3.3)

### **3.3 Critical parameters for discrimination**

Discriminating individuals included a range of 6 temporal, frequency and descriptive measures; F0Start, Falling range, interval between pulses, falling slope, no. of bubbles and no. of volcanoes.

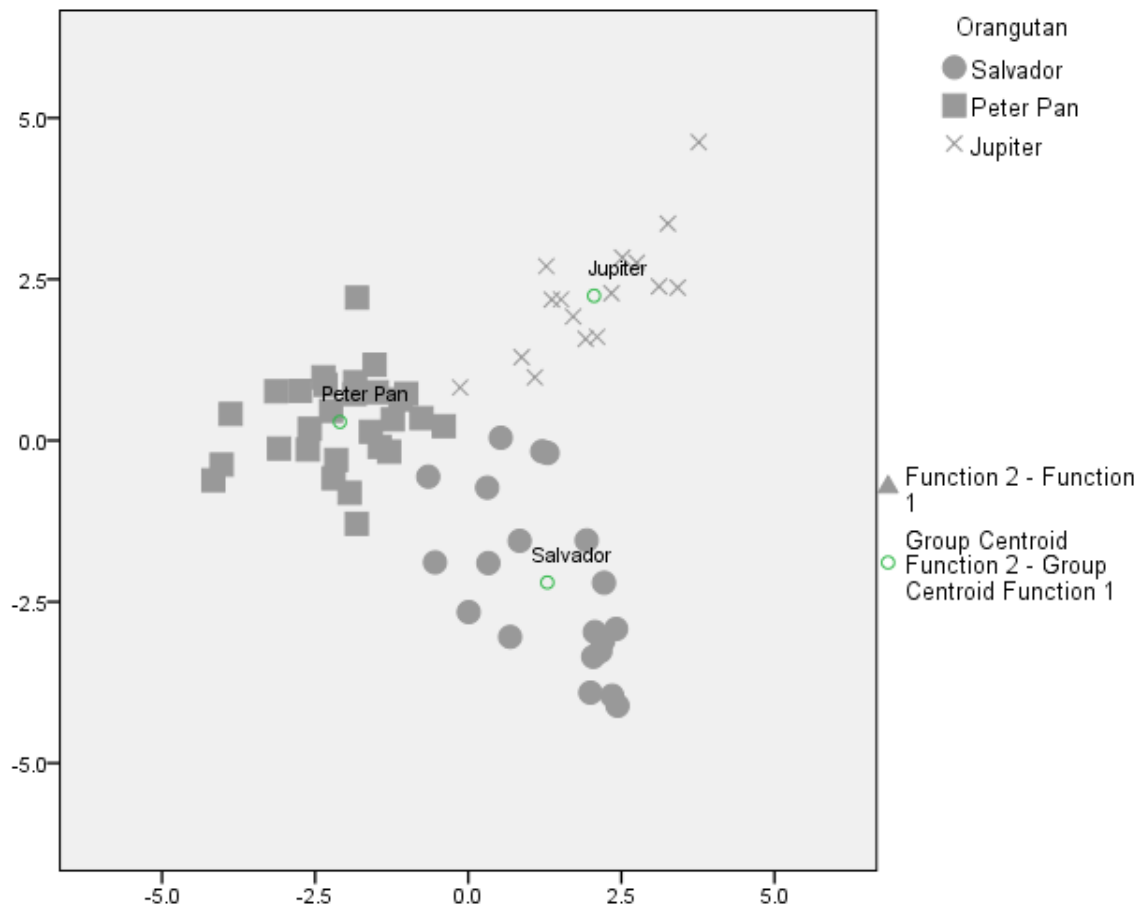
With Peter Pan & Jupiter's data split and Salvador's remaining the same, discrimination was characterised by frequency, temporal and descriptive variables. F0Start, Rising duration, Falling range, interval between pulses, falling slope, call rate, no. of bubbles and no. of volcanoes.

For all four contexts only number of volcanoes was a factor in discrimination. Substantially more occurred under the spontaneous context than any other.

When snag crash and response call were combined to make the context "aroused" discrimination was characterised by 2 descriptive measures, No. of volcanoes and sigh, and 2 frequency measures, falling slope and falling range.

**Table 3. Discriminant function analyses for individuality and context**

|                                       |                        |                   |           |          |
|---------------------------------------|------------------------|-------------------|-----------|----------|
| <b>Individuality:</b>                 |                        |                   |           |          |
| <b>Dimension</b>                      | <b>Canonical corr.</b> | <b>Chi-square</b> | <b>DF</b> | <b>P</b> |
| 1                                     | 0.886                  | 170.416           | 12        | <0.001   |
| 2                                     | 0.864                  | 80.28             | 5         | <0.001   |
| <b>Individuality with year</b>        |                        |                   |           |          |
| <b>Dimension</b>                      | <b>Canonical corr.</b> | <b>Chi-square</b> | <b>DF</b> | <b>P</b> |
| 1                                     | 0.9                    | 238.44            | 32        | <0.001   |
| 2                                     | 0.873                  | 144.75            | 21        | <0.001   |
| 3                                     | 0.766                  | 63.41             | 12        | <0.001   |
| 4                                     | 0.462                  | 13.55             | 5         | 0.019    |
| <b>All contexts:</b>                  |                        |                   |           |          |
| <b>Dimension</b>                      | <b>Statistic</b>       | <b>Chi-square</b> | <b>DF</b> | <b>P</b> |
| 1                                     | 0.78                   | 14.051            | 3         | 0.003    |
| <b>Aroused vs. Female/Spontaneous</b> |                        |                   |           |          |
| <b>Dimension</b>                      | <b>Canonical corr.</b> | <b>Chi-square</b> | <b>DF</b> | <b>P</b> |
| 1                                     | 0.661                  | 45.362            | 8         | <0.001   |
| 2                                     | 0.464                  | 13.48             | 5         | 0.004    |



**Chart 1. A scatter plot of for each orang-utans different scores against functions 1 & 2, which comprise F0Start, Falling range, interval between pulses, falling slope, no. of bubbles and no. of volcanoes.**

### 3.4 Call direction, subsequent travel direction & context

Call direction was a strong predictor of both initial direction and overall direction of travel across the contexts. However, was not significant under the two aroused contexts alone. Under spontaneous conditions alone, however, its significance as a predictor increased, with a female it remained at a similar level (Table 4).



Table 4. Regression analyses of direction and direction of travel

| Context         | Travel  | R <sup>2</sup> | F <sub>(dfx,dfy)</sub> | $\beta$ | t      | p        |
|-----------------|---------|----------------|------------------------|---------|--------|----------|
| Overall         | Initial | 0.731          | (1,73) 198.26          | 1.047   | 6.546  | p<0.001. |
|                 | Overall | 0.716          | (1,73) 186.41          | 0.910   | 13.509 | p<0.001. |
| Spontaneous     | Initial | 0.8            | (1,42) 168.52          | 0.885   | 12.982 | p<0.001. |
|                 | Overall | 0.742          | (1,42) 121.07          | 0.871   | 11.003 | p<0.001. |
| With snag crash | Initial |                |                        |         |        | N.S      |
|                 | Overall |                |                        |         |        | N.S      |
| Response        | Initial |                |                        |         |        | N.S      |
|                 | Overall |                |                        |         |        | N.S      |
| With female     | Initial | 0.716          | (1,17) 42.855          | 1.047   | 6.546  | p<0.001. |
|                 | Overall | 0.775          | (1,17) 58.397          | 0.731   | 7.642  | p<0.001. |

## **4. Discussion**

### **4.1 Individuality**

The results of this study indicate that there are a number of differences in the acoustic structure of long calls produced by different male orang-utans. While this doesn't automatically preclude the assumption that an audience is able to use these differences to identify the calling male, or even that they are capable of doing so, it does mean that there is the potential for individual recognition by receivers of both sexes. While orang-utans are largely solitary, they do, on occasion, encounter conspecifics, with interactions heavily dependent on the sex and relative status of the individual involved; male-male encounters are often highly aggressive and inter-sexual encounters can take a similar path, with forced mating common even when dominant males are involved, though evidence suggests that females tend to preferentially mate with a dominant individual (Utami Atmoko et al., 2009).

It seems therefore advantageous for a receiver to identify the caller beyond visual contact as this would allow them to avoid potentially hazardous encounters with harmful males and actively seek advantageous interactions. Evidence for this has been illustrated by both observational (Delgado, 2003; Mitra Setia & van Schaik, 2007; Spillmann, 2010) and playback (Mitani, 1985b; Delgado, 2003) experiments, where subordinate males have been shown to avoid the calls of a dominant male and vice versa, while females have been shown to always approach the call of a dominant male regardless of reproductive status.

However since none of these studies were undertaken with the Sabangau population, and only one was on Bornean orang-utans, it is necessary to establish if, as seems likely, this population

does indeed discriminate between individuals and how this is manifested through observational and playback methods.

It was additionally interesting to note the ability to distinguish from one year to another. This is potentially important, because it indicates that the orang-utans state is changing, and that the long call may change along with state indicating that it is a reliable indicator of quality.

However, despite this possibility, it should be noted that in 2007 when some of the recordings were made Jupiter was in extremely poor condition, with a low body weight, shrunken cheek pads and neck sack, (Morrogh-Bernard, Personal Communication) yet the discriminant function analysis showed little difference between three years ago and now, where he was in very good condition. Conversely Peter Pan has been dominant for the last three years, yet his long call has changed substantially. This could indicate that the acoustic structure of long calls reflects dominance rather than physical condition or perhaps that there is an element of learning and development, though much further analysis is required into the long calls of orang-utans made over a long period of time, alongside measures such as dominance rank and health correlates.

## **4.2 Context**

While the discriminant analysis of the overall contexts was marginally significant explaining some variance, there was only one variable having an impact upon this variation, that of number of volcanoes. This is contrary to previous studies on orang-utans and other primates which have found temporal variables to be most crucial for determining between contexts (Wich et al., 2003; Spillmann et al., 2010). I believe this is probably due to the small sample size being dominated by spontaneous long calls, which contain a significantly higher number of volcanoes (mean = 20, next highest = 3) than any other context. It would be useful therefore to obtain a larger

sample, therefore increasing the number of less common contexts, such as with female that can be compared to spontaneous.

Despite this, when snag crashing and response calls were combined the discriminant values went up, suggesting that these two contexts invoke the production of a similar long call. The difference between these aroused calls has been documented for a number of species including chimpanzees (Notman & Rendall, 2005), langurs (Wich et al., 2003) and most relevantly orang-utans (Spillmann et al., 2010). However in all of those, temporal variables were the major discriminating factor and while there was a trend towards it being higher under aroused contexts, there was no statistical significance. Again further work is needed.

It should also be noted that the addition of an extra context in comparison to those used by Spillmann et al., (2010) that of with a female, did not seem to affect the results as context remained significantly identifiable. I think that with a female is probably one of the more common contexts, is likely to invoke a different long call due to the orang-utan not wanting to alert conspecifics, but alternatively wanting to impress, and it was very interesting to note the females' responses to the males calling (see below).

#### **4.3 Call direction, subsequent travel direction & context**

The orang-utans at Sabangau appear to “announce” their direction of travel by facing the direction in which they intend to travel when calling, both in terms of initial travel and over the longer period between calls. This correlates with anecdotal evidence from both Bornean and Sumatran sites (van Schaik, unpublished). Potentially, the drop in explained variation from initial and overall direction of travel is explained by the likelihood of an individual encountering a distraction between calls, such as a preferred food item or a conspecific, which will cause the orang-utan to deviate from its initial path.

The impact of context is further illustrated by these results, while spontaneous call or one made in the presence of females indicate the direction of travel, those made in response or with a snag crash do not, supporting the hypothesis that these contexts have a different function (see section 4.2). These findings potentially indicate that when made spontaneously the long calls are being used as a mechanism to maintain a co-ordinated network of dispersed individuals centred on a dominant male, when present (MacKinnon, 1974; Delgado, 2003; Delgado, 2007), again this is supported by Spillmann et al.'s (2010) finding that oestrous females moved towards spontaneous calls, while those with infants moved away, yet did not perceptibly react to calls made under other contexts.

Interestingly, the observers in this study noted that when the orang-utans called in the presence of a female, in most cases the female would immediately come to the male. Potentially, therefore, these calls could serve as an indication of sexual receptiveness or perhaps function to keep the group together by indicating where the dominant male intends to move (Morrogh-Bernard, in prep.).

To date, this indication of future travel has no known counterpart among non-human primates, and suggests orang-utans have prospective cognition of future travel direction. Although males are, more often than not, alone when producing a long call, and therefore the receiver is not necessarily aware of what direction the caller is facing, evidence points to listeners being able to determine a conspecifics relative position from their call (Mitani, 1985a) and perhaps through experience are even able to determine their subsequent direction of travel. Clearly, further study is required into receivers' behavioural responses and subsequent travel direction when hearing calls made under different contexts and directed towards or away from them to assess the potential functions.

## 5. Conclusions

Until now long calls have been thought of as functioning in male spacing and mate attraction (Mitani, 1985b; Delgado, 2003; Spillmann et al., 2010). My results provide evidence for both hypothesis and agree with Spillmann et al.'s (2010) conclusion that the function may differ according to the context under which the call is made.

The two hypotheses are not exclusive and it seems likely from my results and those produced by other researchers that the long call has a number of functions. This is supported by my finding distinct acoustic differences between long calls made under different contexts, suggesting the function may change with the situation. In support of the male spacing hypothesis is my finding that orang-utans call in the direction they will travel an exciting discovery that does lead towards interesting questions about the cognitive abilities of both the caller and receiver. However, for any of these hypotheses about the long calls function to be feasible, there is the initial requirement that the long calls must be distinguishable from one individual to another. It is, therefore, more important as a building block for future work that this study has established the long calls produced at Sabangau do contain sufficient variation to allow for identification of an individual.

In conclusion it seems apparent that both individual and contextual differences are advertised by flanged male orang-utans through their long calls. These individual and contextual differences may allow receivers to approach or avoid the caller, according to the costs or benefits of doing so, and are able to assess a male without having seen them. Through this mechanism it seems likely that orang-utans both attract mates and regulate the spacing of males. Furthermore orang-utans appear to utilise the long call to advertise their future direction of travel and perhaps through this are able to co-ordinate a network of dispersed individuals. However it should be noted that the sample size of this study is very small and that further study

is needed to evaluate these findings, both in terms of repeating the methods used and by taking it a stage further with experimental playbacks and behavioural observations on orang-utans of different sexes and ages, if we are to fully understand the function of their long call.

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