Tinder for orang-utans: comparing sexually selective cognition among Bornean orang-utans (Pongo pygmaeus) and humans (Homo sapiens)

Roth, T.S.

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Chapter 8

Evidence of female proceptive behaviour and vocalisation during ovulation in two zoo-housed Bornean orang-utan (*Pongo pygmaeus*) females

Abstract

In some primate species, females show changes in proceptive behaviour across the menstrual cycle. This anecdotal report discusses the occurrence of ovulation-induced proceptivity and vocalisations in two zoo-housed Bornean orang-utan females. Observations of two individuals, Temmy and Eloise, during their peri-ovulatory periods revealed distinct behavioral patterns. While Temmy demonstrated male-seeking behaviour and vocalisation in response to playbacks of male long calls, Eloise consistently solicited the male she was housed with and proactively produced vocalisations during her ovulation. Interestingly, the vocalisations produced by Temmy and Eloise seem to differ in many aspects from known orang-utan calls, although they bear some similarities to male long calls. Thus, the vocal repertoire of female orang-utans may be more extensive than previously thought. We carefully suggest potential functions of female proceptivity calls, while also outlining how such calls could be detrimental for orang-utan females. Furthermore, we consider the possibility that these vocalisations are only present in captive orang-utan populations.

Based on:

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Data availability statement

The datasets and materials generated and/or analysed during the current study are available via Dataverse: https://doi.org/10.34894/JNUTYU

Introduction

Primate females can substantially change their sexual behaviour across the menstrual cycle. According to Beach (1976), these changes in behaviour can be divided into three categories: attractivity, receptivity and proceptivity. Attractivity refers to the stimulus effect of the female on males. For example, genital swelling might increase attractivity of a female (Dixson, 2012). Proceptivity refers to female appetitive sexual behaviours, such as approaching males, vocalising, presenting, and affiliation with males. Receptivity concerns behaviours that facilitate copulation, such as employing the correct body postures (Hrdy & Whitten, 1986). In some primates, increases in attractivity, proceptivity and receptivity concord with the occurrence of ovulation. However, sexual behaviour in primates is not rigidly controlled by ovarian hormones and most female primates engage in mating throughout the menstrual cycle. Therefore, the relationship between fertility and sexual behaviour is not always straightforward in primates (Dixson, 2012).

Orang-utans (genus *Pongo*) are among the primate species for which there is evidence consistent with the idea that female sexual behaviour changes across their 30-day menstrual cycle. While recent evidence suggests that attractivity and receptivity do not change substantially across the cycle (Durgavich et al., 2023), data from both captive and field studies suggest that orang-utan females show a change in proceptivity across their menstrual cycle. In captivity, a zoo-housed Sumatran orang-utan (*Pongo abelii*) female showed a 4-6 day-lasting increase in proceptive behaviour, such as following, grooming, and touching the genitals of the male (Maple et al., 1979). According to the authors, these periods occurred approximately 26-30 days apart, which suggests that they coincided with ovulation. Similarly, in a restricted access study, orang-utan females were proceptive towards males specifically during their ovulation: when females had control over access to males, they chose to spend time with the male mostly during their ovulation (Nadler, 1995). Furthermore, field data suggest that Bornean orang-utan females (*Pongo pygmaeus*) show a qualitative change in proceptivity across their menstrual cycle (Knott et al., 2009): females seemed to make no distinction when mating with either flanged or unflanged males when they were not fertile, but specifically mated with dominant flanged males during ovulation. Altogether, these results suggest that orang-utans show qualitative and quantitative changes in proceptivity that co-occur with ovulation.

Orang-utans are also characterised by long calls: acoustic signals that are produced by flanged males or males who are developing flanges (Delgado et al., 2008). These calls reach a loudness of approximately 100 decibels (Lameira & Wich, 2008) and carry for about 1km (Mitani, 1985). These calls are thought to play an important role in regulating social interactions (Delgado et al., 2008), given that orang-utans are semi-solitary and only sporadically interact with conspecifics (Roth et al., 2020; van Schaik, 1999). Two main functions have been suggested, which are not mutually exclusive (van Schaik & van Hooff, 1996); first, long calls might facilitate inter-individual spacing, especially between males (Delgado et al., 2008; Mitani, 1985). Second, long calls might function to attract females (Mitra Setia & van Schaik, 2007). Accordingly, Mitra Setia & van Schaik (2007) reported that females approached male long calls, and especially the calls of local dominant males. Altogether, it seems that long calls do not only play a role in intrasexual competition, but also in intersexual competition.

When it comes to female vocalisations in the context of mating, remarkably few examples of proceptive vocalisations have been described in primates (Dixson, 2012). This also applies to orang-utans. Hardus et al. (2008) describe two vocalisations that females produce during copulation: mating squeals and fear squeals. However, we have found no mentions of proceptive vocalisations, i.e., vocalisations that precede mating events. Nonetheless, production of proceptive vocalisations might be beneficial for orang-utan females, through either coordinating movement with preferred males (long- or intermediate-distance calls) or communicating their intention or motivation to mate (short-distance calls) in order to reduce male ambivalence towards them (O'Connell et al., 2020). Especially in habitats with bad visibility vocalisations can aid in coordination and social interaction (Delgado, 2006) and reduce ambiguity during social approaches.

Here, we report two cases of increased proceptivity in ovulating zoo-housed Bornean orang-utan females. Our first case concerns Temmy, who showed a strong bodily and vocal response to male long call playbacks. We observed this phenomenon during a playback experiment in which she at first did not participate. She was temporarily housed in the outside enclosure while we conducted our playback experiment in the indoor enclosure, and was likely in her peri-ovulatory period. We opportunistically played long call recordings on 4 consecutive days while she was in the outdoor enclosure and videorecorded her behaviour. Approximately 2 months later, we repeated this on two consecutive days when she was most likely not ovulating. Our second case concerns Eloise, who appeared to produce long calls spontaneously during ovulation when she was still reproductively active. In this anecdotal report, we (1) describe the behaviours of Temmy and Eloise, and (2) describe the structure of their vocalisations.

Method

Temmy

Group and housing

Data for the first case were gathered in Allwetter Zoo (Münster, Germany). During the first study period (23-05-2022 until 27-05-2022), the zoo housed five adult Bornean orang-utans (4F, 1M; Supplementary Table 1). During the second study period (29-07-2022 until 30-07-2022) a new male was also present, who had recently been transported to the zoo. The orang-utan enclosure consisted of an indoor and outdoor enclosure, each capable of housing a subgroup. Alternatively, they could be connected to form one large enclosure.

Temmy, the female of interest in this case, had been living in Allwetter Zoo for over 20 years at the time of research. She had not been exposed to a flanged male since the death of the previous flanged male at the start of 2020. During the first study period, Temmy was housed solitarily in the outside enclosure until ±15.30, when Mr. Miyagi was also allowed to move to the outside enclosure. During the second study period, Temmy and unflanged male Mr. Miyagi were housed together (either in the indoor or the outdoor enclosure), while the rest of the group was already introduced to the new flanged male Ramon.

Female ovulation

While we lack hormonal evidence of ovulation, multiple lines of evidence suggest that Temmy was ovulating during our first observation period. Firstly, because of a breeding recommendation by the EEP, Temmy was not on contraceptives. Secondly, according to the curator and the orang-utan caretakers, Temmy started the peri-ovulatory period of her menstrual cycle right before the first study period. Thirdly, the caretakers had observed a cooperative mating event between Mr. Miyagi and Temmy on the evening of 22-05-2022, two days prior to the start of our study. While sexual activity is not restricted to the peri-ovulatory period, it is much more likely to occur during this period (Durgavich et al., 2023). In orang-utans, this part of the cycle lasts approximately 5 days, similar to humans (Kubatova & Fedorova, 2016).

Stimuli

The long call recordings that we used for the playback experiment were collected at Sikundur Research Station (Sumatra, Indonesia) by James Askew (Askew, 2019). From all the recordings, we selected only calls classified as "spontaneous". As control sounds we used two calls of the Great argus pheasant (*Argusianus argus*), a bird species that occurs in the natural habitat of orang-utans. We edited all stimuli to last 45 seconds so that each stimulus had the same duration. Furthermore, all recordings were normalized so that the volume level was similar across stimuli.

Design of trial

We made audio recordings of the vocal response using a Sennheiser ME 67 microphone and a Tascam DR-40X recorder. Two camcorders (study period 1) or one camcorder and one action camera (study period 2) were used to videorecord the behavioural response to the stimuli. To play the stimuli, we used a custom loudspeaker linked to a Marantz PMD 620 unit. We played the stimuli at ±90 dB at 1 m from the loudspeaker.

The setup of our study was in line with recommendations (Fischer et al., 2013): while one researcher was responsible for placing the speaker and playing the sound, one or two other researchers videorecorded the response. In addition, one of the researchers carried the microphone that was used to record Temmy's vocalisations opportunistically. Before starting a trial, we would first identify Temmy's location. After that, we would determine a suitable location for the speaker. We did not want the speaker to be clearly visible to Temmy at the onset of the trial. After we chose a location for the speaker, we would start the stimulus playback of 45s and immediately videorecord her response. We would continue videorecording her response for a few minutes after the stimulus ended, and would stop when her behaviour seemed to be back to baseline (ie., when she displayed no more intensely proceptive behaviours and/or stopped vocalising).

Eloise

Data for the second case were obtained from Los Angeles Zoo (LA, California, United States). This case concerns Eloise, a Bornean orang-utan female who was born in LA Zoo on 10th of November 1968, and has been living in LA Zoo since then. Over time, she has been housed with multiple individuals, including different males. She gave birth to 4 offspring from 3 different males between 1978 and 1987. In our case description, we focus on the period from 1999 until approximately 2018, date after which she is considered to be of post-reproductive age (based on the absence of a regular menstrual cycle). During the period that we describe, she was housed with a flanged male, and with different females. Furthermore, she was not on contraceptives at any time during this period.

Eloise has a condition similar to cerebral palsy, which she has had since birth. Her condition mostly affects her locomotion, since she has limited use of her hands and especially her feet. She has learned over her years how to modify her movements, and has generally locomoted by rolling or crawling. However, she has still been able to have a normal social life with conspecifics, and has been able to climb and manoeuvre throughout her exhibit space.

Importantly, one of the authors of this manuscript (MF) was Eloise's primary caregiver in the zoo during the period that we describe.

Vocalisation analyses

Bioacoustic analyses were performed using Audacity software (Audacity Team, 2011). Measurements were taken of the total call length, inter-onset-intervals of the separate vocalisations, peak frequencies, and fundamental frequencies. Based on these parameters, the vocalisations of Temmy and Eloise were compared to other orang-utan calls obtained from *Orangutan network* of Universität Zurich (https://www.aim.uzh.ch/de/orangutannetwork.html; Hardus et al., 2009). Furthermore, we compared Temmy's and Eloise's call with male long calls recorded by James Askew (Askew, 2019; also see "Stimuli").

Results

Temmy

Study period 1

On the first day (24-5-2022) that we performed a playback experiment in the indoor enclosure with all orang-utans except Temmy, we noted that Temmy showed a strong behavioural reaction through a semi-transparent door that connected the indoor and outdoor enclosure. On this first day, we played 3 control calls, 3 calls of flanged males, and 3 calls of transitioning males. Temmy showed up at the door during/after all playbacks of flanged male long calls, and once after playback of a transitioning male long call (Figure 1). Importantly, she would only come to the door during or after the playback of the long call. Thus, she was never visible at the window at the start of the trial. In addition, she never came to the door in response to the control sounds. Because of her strong reaction to the long call stimuli, we asked permission to opportunistically expose her to some stimuli in the outside enclosure. We started doing this on the afternoon of the first day.

Figure 1. Temmy coming to the door that separates the indoor and outdoor enclosure in response to a flanged male long call.

On the afternoon after we had finished with the indoor trials for the playback study, we played two long calls specifically to Temmy, in the outer enclosure. In both cases she showed a strong behavioural response (Figure 2). Her response to the long calls was characterised by fast movement in the direction of the speaker, climbing into climbing structures, and standing/sitting while looking in the direction of the speaker. Furthermore, Temmy started vocalising for multiple minutes in a row. On the morning of day 2, we resumed playing long calls to Temmy in the outside enclosure. However, we now also included control sounds to determine whether she would show the same behavioural response to all sounds. In total we played three long calls and four control sounds. Temmy showed responses similar to the day before when we played long calls, including vocalisations, but showed no discernible behavioural response when we played a control sound. Crucially, she quickly approached the source of the stimuli and emitted vocalisations in response to calls, but never to control sounds.

On the afternoon of day 2, we wanted to continue the experiment by playing more stimuli to Temmy. In this case, we played two long calls and two control stimuli. Similar to before, she did not respond to the control trials. However, her behavioural response to the long calls was completely different from this moment onwards. While she did still look into the direction of the speaker during the stimulus playback, she did not approach it like before, nor vocalise. In the next two days, we played three more long calls and three more control stimuli, but Temmy did not respond like she did on day 1 and the morning of day 2 anymore.

The change in behavioural response that we observed suggests that Temmy only showed proceptive behaviour in response to the calls during her peri-ovulatory phase. Given that this phase lasts about 5 days, this fits well with the fact that Temmy and Mr. Miyagi mated two days prior to the study period. However, another explanation would be that Temmy habituated to the stimuli over time, even though this would not explain why she did not show a similar response to the control stimuli. Still, we went back 2 months later to test this alternative hypothesis.

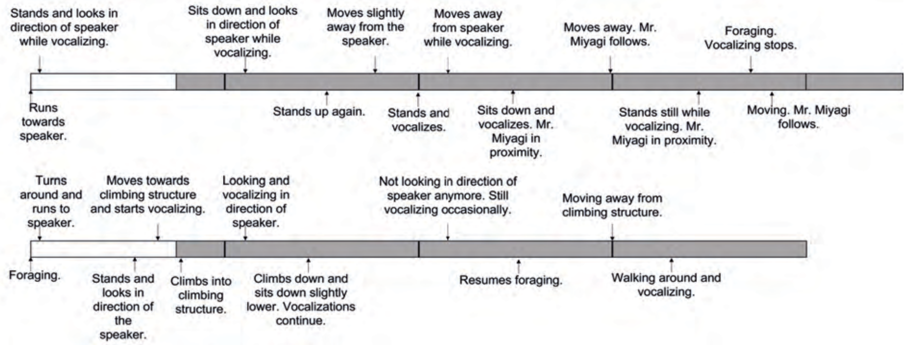

Figure 2. Description of the behavioural responses of Temmy to the long call stimuli on day 1 of the first study period. The white bar represents the duration of the stimulus playback, while the shaded bar represents the post-stimulus period. The area between two thick black lines represent one minute.

Study period 2

66 days after the first study period, we returned to Allwetter Zoo, and played a few more long call recordings and control sounds to Temmy while she was -most likely- not ovulating. If her strong behavioural responses were the result of a novel sound, and the relaxation of her response over time the result of habituation, we would expect to see a strong response to the long call stimuli after 66 days of no exposure to the stimuli. If the behavioural responses were caused by ovulation, however, we would expect to see no noticeable response during the second study period.

The results from the second study period match with the latter: Temmy did not show the strong behavioural response that she showed during the first study period. In total, we played her seven long call stimuli and five control stimuli in two days. The only noticeable response to the stimuli was that Temmy sometimes looked towards the speaker while the stimulus was played, but she did not vocalise or walk towards the source of the stimuli as she had done at the beginning of study period 1.

Eloise

Our second case concerns Eloise, a Bornean orang-utan female living in LA Zoo. To our understanding, she had been producing vocalisations during ovulation since she became of reproductive age. Although no consistent records exists with regard to this specific behaviour at earlier stages of her life, one of the authors (MF) has worked as her main caregiver since 1999, and observed that she consistently produced vocalisations during ovulation until approximately 2018. The vocalisations consistently co-occurred with ovulation, as evidenced by the fact that Eloise consistently produced the vocalisations approximately two weeks after onset of her menstruation on a monthly basis. Furthermore, her vocalisations coincided perfectly with increased proceptivity towards the flanged male that she was housed with, reflected in following the male and actively soliciting him.

During ovulation, Eloise would actively pursue the male, while outside of her ovulation timeframe she would not actively seek him out. This would include her following him throughout the exhibit space; when he would move areas, she would actively follow. She would also position herself for copulation, trying to solicit a response from the male. The male would copulate with Eloise, and would occasionally want to be housed with her overnight. Given Eloise's condition, she was subordinate to the other females in the group. If any of the other females were ovulating at the same time as Eloise, she would be supplanted and pushed away by the females. Otherwise, these females would not intervene. Her ovulation lasted approximately 3-4 days, with the vocalizations being most intense during the first day or two of the cycle and slowly tapering off.

The fact that her vocalisations started 2 weeks after her menstruation, and coincided with an increase in proceptivity as well, suggests that the vocalisations were induced by ovulation. This conclusion is further supported by the fact that disappearance of the vocalisations co-occurred with Eloise's transition towards her post-reproductive period. Thus, when Eloise's menstrual cycle became less regular, her calls became less frequent and eventually disappeared.

Vocalisation analysis

During all playbacks that we performed in the period of study 1 for which we suspect Temmy was in the peri-ovulatory period, Temmy performed vocalisations. We were able to capture three good quality recordings of the vocalisation that Temmy produced. These calls consisted of short series of 5 to 6 consecutive bark-like vocalisations (hereafter pulses; Figure 3). Each call lasted on average 4.2 seconds (SD=0.3), in the longest recording these calls were repeated consecutively for more than 3 minutes. Each bark-like pulse within the call had an average duration of 690ms long (SD=48ms), with an average fundamental frequency of 250 Hz. These parameters remained consistent across all of Temmy's vocalisations. Only the intensity of the calls decreased sharply after 65 seconds of vocalising. Still, the softer calls remained similar in the other acoustic parameters.

Interestingly, the calls that Temmy emitted in response to the playbacks seem to be different from any calls generally known to be uttered by orang-utans. To validate this, we compared Temmy's calls to known sounds in the orang-utan repertoire: the grumble, complex call, rolling call, gorkum and lork call. These comparisons were based on 4 main features, call duration (s), peak frequency (Hz), fundamental frequency (Hz) and inter-onset-interval length (s) (Figure 3). The complex call, rolling call and gorkum all have one high frequency burst in the 3500 Hz range, something that is missing from Temmy's vocalisations during the playbacks. However, based on the temporal structure, these calls are rather similar. Temmy's vocalisations might be a variation on the complex call that lacks the high burst and where the emphasis is mainly on the low-frequency grunts. Based on the frequency range, there is more similarity with the grumble, a call with a quick repetition of short and low pulses. These same pulses seem to occur in Temmy's vocalisations. However, Temmy's are higher in frequency (250 instead of 150 Hz) and occur in more tightly knitted sets. The lork call seems to be most similar to Temmy's vocalisations. Both are relatively long calls (>60 seconds) with low frequency pulses. Nevertheless, the lork calls are much slower than Temmy's vocalisations. Both the separate pulses as well as the pauses between these pulses are about double the length in the lork calls than in Temmy's vocalisations. This means that these vocalisations of Temmy in response to the male long-call share features of some of the known calls from the orang-utan repertoire but bear no complete similarity to any of them.

Temmy's vocalisations seem to be most similar to the long-calls of male orang-utans (Figure 4). Male long calls also consist of bark-like pulses that average around 800ms each (average IOI of 1.5 sec) with a fundamental frequency of around 320 Hz. An analysis of the spectral information also shows that most of the power in these calls occurs in the same spectrum, between 200 and 350 Hz, with little to no power in the higher frequencies. With regard to the temporal structure, these calls bear strong resemblance in the sound onset timing. In addition, the duration of each pulse is similar between Temmy's vocalisations and male long-calls. Temmy's pulses have inter-onset-intervals (IOIs) of approximately 740ms (SD=61ms), whilst the 12 male long calls that we analysed have IOIs of approximately 800ms (SD=54ms). The clearest difference between Temmy's vocalisations and the male long-calls lies in the overall temporal structure. Long-calls consist of rather regular repetitions of pulses that can last up to 3 minutes with steady IOIs. Temmy's calls could also last up until 3 minutes in total, but with concatenations of bouts of 5-6 pulses, followed by a longer pause (+/- 2,5 sec.) before there was another pulse-bout. The IOIs within these bouts are similar to male long-calls, but the pauses between bouts are not typical for long-calls. To conclude, Temmy's call seems to be most similar in temporal structure and frequency distribution to the male long-calls and less so to other orang-utan vocalisations.

A second female, Eloise, proactively produced calls that also bear similarities with male long calls. Rather than the reactive calls of Temmy to long-call playbacks, this female produced long-call-like calls spontaneously. Eloise's calls mainly differ from Temmy's with respect to timing. Each pulse is much longer, with an average of 2.237 sec per pulse (average IOI 2.467 sec.). This makes her pulses also longer than those of the male long-call. However, unlike the concatenated pulse-bouts in Temmy's calls, Eloise's full calls retained a regular IOI pattern for

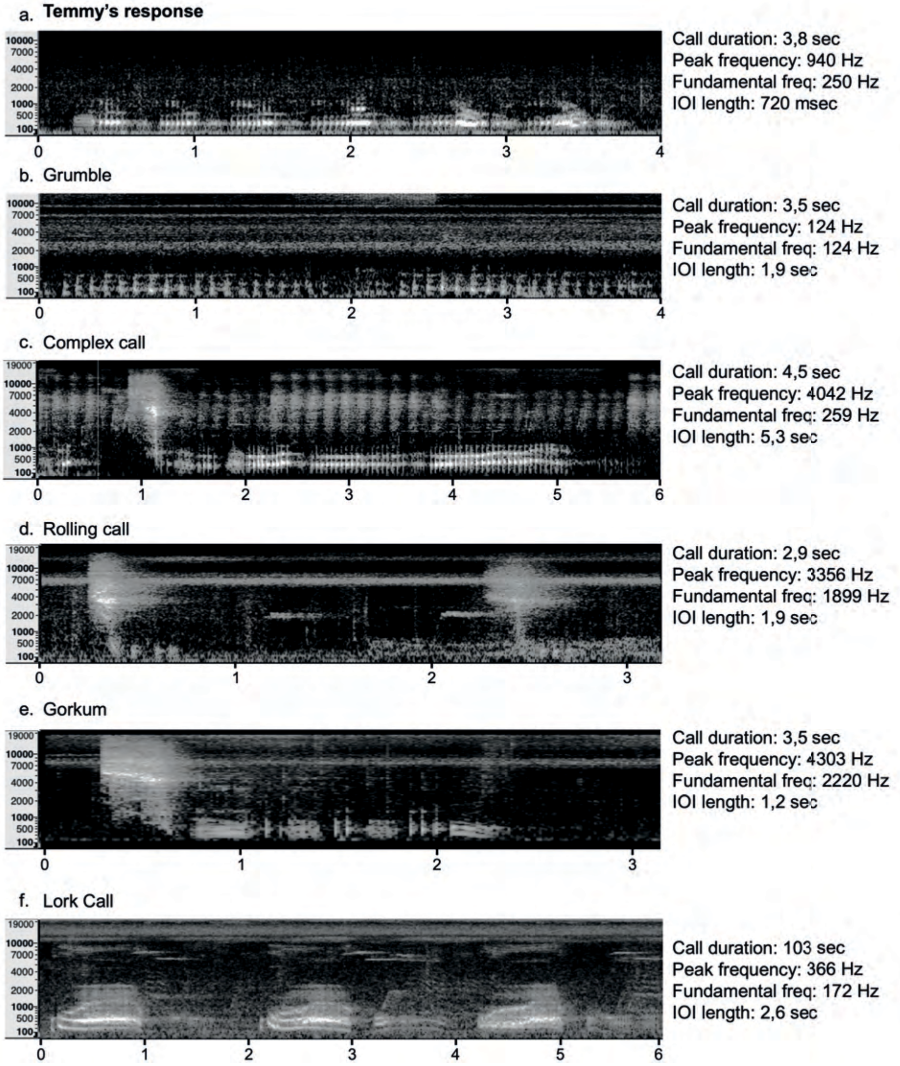

Figure 3. Comparison between Temmy's vocal response to other vocalisations known in the orang-utan repertoire. Analysed aspects of the vocalisations were: total call duration (s), Peak frequency (loudest frequency of the call), fundamental frequency (lowest frequency of the call), Inter-onset-interval (time between start of one vocalisation to start of next vocalisation within the call). B-f indicate 5 different orangutan calls that bear certain similarities to Temmy's vocal response. Neither of them can be categorized as the same call that Temmy is producing.

the whole duration. One call could continue for up to 60 seconds with steady IOIs, which bears more similarity to the long stable duration of the long-calls which generally last between 60 and 120 seconds. With respect to the fundamental and peak frequency, Eloise's calls were closer to the male long call compared to Temmy's (average Eloise fundamental frequency: 300 Hz, male long-call around 350 Hz, Figure 5).

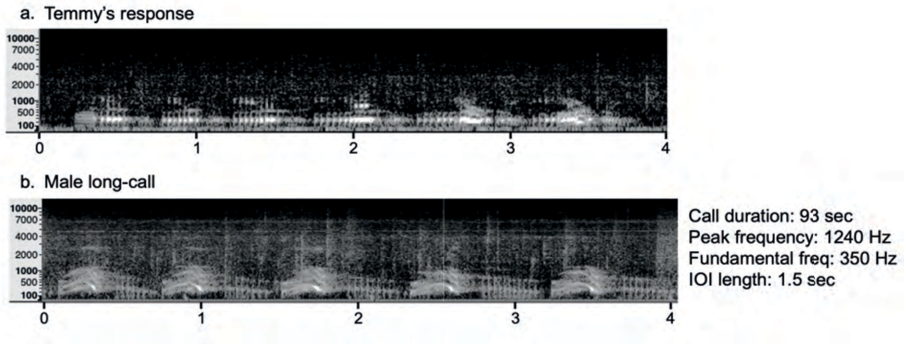

Figure 4. Male long-call spectrogram in comparison with Temmy's vocal response. Male long-calls have a longer total duration than Temmy's vocalisations, but the pulses bear many resemblances in spectral and temporal pattern.

In comparison to the known repertoire of orang-utans, it is noticeable that these calls bear less resemblance to these known vocalisations. It might come closest to the complex call which has also relatively long and low call units. However, the units in the complex call are produced as several short, consecutive bursts, whilst the long-call-like call of Eloise is one long burst on an exhale, followed by an audible inhale. Especially the long duration of the pulses and the total call duration of Eloise's vocalisations make them incomparable to any of the known orangutan calls.

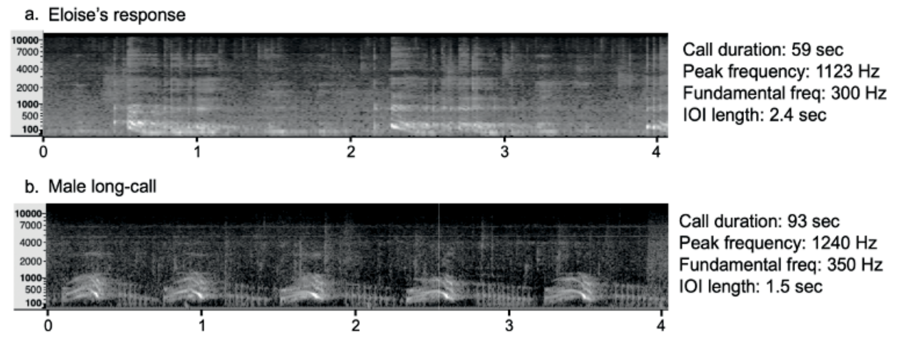

Figure 5. Eloise's vocalizations in comparison to the male long-call. The pulses in Eloise's call are longer than those of the male-long call. However, the overall call structure and total call length are similar. The spectral information of the call also bears many similarities to the male long-call.

Discussion

In this anecdotal report, we describe two cases of ovulation-induced proceptivity and vocalisation in zoo-housed Bornean orang-utans. First, we described the case of Temmy, who was likely ovulating when we opportunistically played long call recordings to her. She showed a strong bodily and vocal response to these calls, but her response disappeared after two days. A follow-up experiment suggests that her change in response did not seem to be driven by habituation. Second, we described the case of Eloise, a female who consistently produced specific vocalisations during ovulation, paired with increased proceptivity towards the male she was housed with. When she reached post-reproductive age, she ceased producing this vocalisation. Even though we want to emphasize that anecdotal reports should be interpreted with caution (Sándor & Miklósi, 2020), our report suggests that changes in orang-utan female's behaviour and vocal repertoire might reflect proceptivity during ovulation. Below, we discuss possible implications for our understanding of the role of female orang-utan behaviour in facilitating mating in captivity and in the wild.

As mentioned in the introduction, previous studies have described that orang-utan females show changes in proceptivity across their menstrual cycle. Our results further substantiate this pattern. We observed how Temmy responded very strongly to male long calls during her ovulation. She actively approached the source of the sound, while she did not do this during control trials. Furthermore, this behaviour was not observed outside of her peri-ovulatory period. Her behavioural response seems to suggest male-seeking behaviour, which would be especially relevant for a semi-solitary species like Bornean orang-utans. Such ovulation-dependent male-seeking behaviour has previously been described in other mammal species (rats, *Rattus norvegicus*: Nofrey et al., 2008; sheep, *Ovis ammon*: Sutton & Alexander, 2019). More specifically, in some primate species females actively seek proximity with males during ovulation (reviewed in Dixson, 2012). Our observations of Temmy suggest male long calls might induce male-seeking behaviour in ovulating orang-utan females, which could results in proximity with preferred flanged males. Some studies on wild orang-utans provide indirect evidence for this: Sumatran orang-utan females seem to approach long calls irrespective of their reproductive state (Mitra Setia & van Schaik, 2007), while in Bornean orang-utans only sexually active females without dependent infants approached long calls (Spillmann et al., 2010). However, these studies did not account for ovulatory status. Therefore, it remains to be established whether wild orang-utan females indeed show a stronger approach tendency during ovulation, like Temmy did. Nevertheless, Knott et al. (2009) suggest that ovulating females show an increase in encounters with in flanged males, resulting in more copulating events with them. Thus, male long calls might be an important stimulus that guides ovulating females towards preferred flanged males, and future studies can further elucidate the mate attraction function of long calls by comparing female responses to male long calls at different points during their menstrual cycle.

Eloise's case supports the notion that ovulating orang-utan females have an important role in facilitating mating. In the period that we described, Eloise showed proceptive behaviour in the form of following the male and actively soliciting him. This is in line with results from restricted-access tests (Maple et al., 1979; Nadler, 1995): when orang-utan males have free access to females, mating events are quite evenly spread across the menstrual cycle. However, when females can control access, they specifically approach males during ovulation. This is also supported by the fact that wild orang-utan females selectively mate with flanged males during their peri-ovulatory period (Knott et al., 2009). Thus, it might be the case that matings are mostly characterised by receptivity outside the peri-ovulatory period (Durgavich et al., 2023), while they are characterised by increased proceptivity followed by receptivity during the peri-ovulatory period. These proceptive behaviours could include actively approaching long calls, following males, and soliciting. In addition, ovulation-induced vocalisations could be considered proceptive behaviours.

Up until now, relatively few vocalisations have been described that are unique to orang-utan females (Hardus et al., 2008). Two of these unique vocalisations occur in the context of mating, namely the mating squeal and the fear squeal. However, to our knowledge, there are no descriptions of female ovulation calls. In this report, we described two seemingly new vocalisations that could possibly be considered ovulation calls. Both Temmy and Eloise produced vocalisations that showed resemblances in spectral and temporal pattern to the male long call. However, Temmy's vocalisations seemed to travel a relatively short distance, while Eloise's vocalisations seem much louder, and could be considered middle- or even long-distance calls (*sensu* Hardus et al., 2008). As far as we know, only one other female long-distance vocalisation has been described for orang-utans, namely the *lork call* (Hardus et al., 2008). According to Rijksen (1978) this call might function as an advertisement call, or as an expression of agonistic state.

However, both Temmy's and Eloise's vocalisations seem to differ from the lork call in several aspects. Altogether, our observations suggest that orang-utan females might have a more extensive vocal repertoire that has been assumed.

While we want to be careful to ascribe a function to the vocalisations, we do think it is interesting to provide suggestions. The most likely function of the calls would be mate attraction. Especially for relatively solitary animals like orang-utans, it might be essential to coordinate movement. Long calls have such a coordinative function (Delgado et al., 2008; Mitani, 1985), but it could well be that female vocalisations also contribute. Although proceptive vocalisations seem to be rare in primates (Dixson, 2012), females of at least two other relatively solitary primate species seem to produce proceptive vocalisations that can travel relatively long distances (grey mouse lemur, *Microcebus murinus*: Buesching et al., 1998; aye-aye, *Daubentonia madagascariensis*: Sterling & Richard, 1995). Given that Eloise's vocalisation was relatively loud, the mate attraction hypothesis would be a likely candidate to explain her vocalisations. However, Temmy's call seems to travel relatively short distance. Potentially, short-distance vocalisations like Temmy's communicate mating motivation or induce arousal in males. Such vocalisations have also been described in other primate species (Dixson, 2012). For example, gelada (*Theropithecus gelada*) females produce pre-copulatory vocalisations, especially during ovulation (Roberts et al., 2017). The length of these calls is a predictor of copulation duration (Zanoli et al., 2022), suggesting that these calls are an indicator of female sexual motivation. Thus, female proceptive vocalisations have previously been described in other primate species, and are potentially present in orang-utans.

It is important to note, though, that these functional accounts are also in conflict with an important aspect of orang-utan sexuality, namely concealed ovulation in females. Orang-utan females show no outward indicators of ovulation (Knott & Kahlenberg, 2011). It has been suggested that concealment of ovulation reduces infanticide risk through paternity confusion (Kunz et al., 2022). If concealing ovulation is indeed beneficial for females, ovulation-induced vocalisations could be detrimental. Therefore, it is also possible that ovulation-induced vocalisations have negative fitness consequences, which would explain why such vocalisations have not previously been described in wild orang-utans. Our cases concern two females from the zoo-housed population, and such housing is often associated with changes in selective pressures (Williams & Hoffman, 2009). Specifically, orang-utan females are often housed with only one breeding male in zoos, which might reduce the likelihood of infanticide, while wild orang-utan females need to navigate a more complex social environment, with multiple males that might pose a threat. Thus, while ovulation-induced vocalisations might occasionally be observed in zoo-housed females, they might be under strong negative selection in wild orang-utan populations due to increased risk of infanticide for females who produce such vocalisations.

Studying mating behaviour of orang-utans in the wild is particularly challenging for multiple reasons (Durgavich et al., 2023). First, they are predominantly solitary, which means that only one individual can be observed at a time. Second, individuals often travel outside of the study area or disappear out of the view of the observers, making it difficult to follow the same individual for prolonged periods. Third, the menstrual cycle of orang-utan females is often suppressed, either because they are pregnant, lactating, or have a negative energy balance. Fourth, if a female is cycling, it is difficult to determine whether she is ovulating: there are no clear morphological indicators, and obtaining urine samples from arboreal species can be difficult. In captivity, researchers are confronted with fewer of these limitations. Thus, studies in captivity can prepare us to conduct methodical observations by describing relatively rare behaviours that may nonetheless occur in the wild.

In conclusion, we described two cases of increased proceptivity during ovulation in two zoo-housed Bornean orang-utan females. Both females also produced vocalisations during their peri-ovulatory period. In the case of Eloise, she produced such vocalisations during her ovulation consistently, for multiple years. We want to emphasise that we cannot ascribe a clear function to the vocalisations, given that our report is anecdotal (Sándor & Miklósi, 2020). Nevertheless, our observations open up possibilities that the orang-utan female vocal repertoire might include vocalisations that indicate proceptivity, and might thus be more extensive than previously thought, at least in captivity. However, it remains to be established whether such vocalisations also occur in wild orang-utan females.