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Temporal patterns in Cape fur seal (*Arctocephalus pusillus pusillus*) mother and pup attraction calls

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Abstract. Vocal recognition is widespread in the animal kingdom, and a necessary tool for offspring survival in some groups. Temporal patterns of animal vocalisations can facilitate communication and convey information such as identity, emotional state, or motivation of the caller. While pinniped (i.e., walrus, eared and true seals) vocalisations are generally well studied, and captive pinnipeds show strong timing abilities, little is known about the temporal structure of their calls in the wild. Here, we followed Cape fur seals (*Arctocephalus pusillus pusillus*) during spontaneous search efforts at the Cape Cross Seal Reserve in Namibia. To investigate the temporal and rhythmic patterning of Cape fur seal attraction calls, we analysed call bouts of 80 mothers and 148 pups. We assessed the relative vocal efforts undertaken by mothers and pups by calculating calling rates, inter-call intervals (periods of silence between vocalisations), and the total time spent calling per bout. To explore the rhythmic structure of the calls, we visualised their temporal patterns by plotting the calling events and frequency histograms of the inter-onset-intervals between each two consecutive vocalisations in a bout. A normalized Pairwise Variability Index was calculated for each individual to investigate underlying patterns and compared between mothers and pups. Pups produced more calls per search, vocalised at higher rates, and took shorter breaks between consecutive vocalisations than females. Even though female vocalisations were much longer, there was no significant difference in the total time females and pups spent vocalising per bout. All animals vocalised at seemingly random intervals, with no distinguishable rhythmic pattern, suggesting that these do not encode identity information during mother-pup reunions. However, numerical analysis showed a potential asynchronous patterning within the age classes, possibly used in anti-masking. Our results indicate that Cape fur seal females and pups invest their energy differently during a search, and while their total calling effort is comparable, reunions seem to be driven mostly by the young.

Keywords. Rhythmicity, vocal communication, pinniped, parent-offspring contact, maternal care, energy expenditure.

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Introduction

Mother-offspring recognition is widespread in the animal kingdom, and a necessary tool for offspring survival in some groups. For example, for an unweaned mammal, separation from the mother may result in starvation, presenting a much higher cost of failure in mother-pup reunions for the young (TRIVERS 1974). In species where separation happens often, e.g., during foraging trips of the parent, it can translate into a greater search effort of the pups. For example, during reunions with their mothers, Northern fur seal (*Callorhinus ursinus*) young invest more energy and produce more response calls than the adult females (INSLEY 2001). Similar asymmetry can be expected in other species and contexts where the risk is much higher for one of the age classes.

During lactation, Otariid mothers spend most of their time on foraging trips (e.g., lactating Cape fur seal (*Arctocephalus pusillus pusillus*) females spend 70% of their time offshore (GAMEL *et al.* 2005). Upon return, mothers and pups must find each other in dense colonies, and facilitate reunions using mostly vocal and olfactory cues (see review in INSLEY *et al.*, 2003). Mothers produce individually specific, stereotyped and loud 'pup attraction calls' (PAC; INSLEY 1992; PHILLIPS & STIRLING 2000; CHARRIER *et al*. 2003; MARTIN *et al.* 2021a) to find their young, confirming this recognition by olfactory cues (PHILLIPS 2003; PITCHER *et al.* 2011). Similarly, a pup looking for its mother actively searches the colony while producing 'female attraction calls' (FAC; GISINER & SCHUSTERMAN 1991; INSLEY 1992; MARTIN *et al.* 2021a). Otariid pups learn to recognise their mother's vocalisations within days (e.g., TRILLMICH 1981; CHARRIER *et al.* 2001; PITCHER *et al.* 2010), and females recognise their young in as little as a few hours (TRILLMICH 1981).

Vocal individuality of pinnipeds is coded in the complex composition of their acoustic signals (e.g., CHARRIER & HARCOURT 2006; TRIMBLE & CHARRIER 2011; MARTIN *et al.* 2021b), mainly within the frequency and amplitude modulation patterns, as well as the energy spectrum of the call (see review in CHARRIER 2020). In general, the more colonial the pinniped species is, the more complex its individual recognition systems are (CHARRIER 2020). Therefore, it is possible that additional cues to encode identity are used by highly colonial animals. One such cue can be the temporal or rhythmic pattern of acoustic signals (e.g., SANVITO & GALIMBERTI 2000; BABISZEWSKA *et al.* 2015; GERO *et al.* 2016; MATHEVON *et al.* 2017), such as beat or isochrony with repetitions at precise internals, or more complex rhythms with repeated sub-patterns (see RAVIGNANI & NORTON 2017). Spontaneous rhythmic patterns occur in vocalisations of many animal groups (see RAVIGNANI *et al.* 2014 for a review), and seem to be common among pinnipeds (e.g., SCHUSTERMAN 1977; SANVITO & GALIMBERTI 2000; SANVITO *et al.* 2007; MATHEVON *et al.* 2017; RAVIGNANI 2018; RAVIGNANI *et al.* 2019). Notably, adult harp seals (*Pagophilus groenlandicus*) and pups of harbour *(Phoca vitulina*) and grey (*Halichoerus grypus*) seals seem to time their vocalisations to avoid masking (i.e., affecting perception of one sound by another; SERRANO & TERHUNE 2002; DE HEER KLOOTS *et al.* 2020).

Here, we explore the temporal properties and rhythmic structure of attraction calls produced by the Cape fur seal, the only pinniped resident on the southern African coastline. Cape fur seals live in large, dense colonies throughout their range (KIRKMAN *et al.* 2013), and display a vocal repertoire typical of Otariids, including individually specific attraction calls produced by mothers and pups (MARTIN *et al.* 2021a, 2021b). Cape fur seal pups produce series of stereotyped, high-pitched bleats facilitating reunion with their mothers (FAC; MARTIN *et al.* 2021a, 2021b). Similarly, mothers produce highly stereotyped calls to communicate with their pups at long or short distances (PAC; MARTIN *et al.* 2021a, 2021b). They have excellent visual timing abilities (HEINRICH *et al.* 2020), which suggests a cognitive ability to keep and/or adjust rhythm. The aim of this study was to describe the temporal patterning of Cape fur seal mothers' and pups' attraction calls, and investigate whether these hold a stereotyped rhythmic structure, with possible implications for anti-masking or individuality coding (i.e., conveying information about the caller's identity).

Methods

Data collection

Data were collected at Cape Cross Seal Reserve, Namibia (21°48′ S, 14°1′ E), between the 3rd and 9th of April 2019. Cape Cross hosts one of the largest Cape fur seal colonies, with tens of thousands of new pups every year (KIRKMAN *et al.* 2007). At the time of data collection, most of the pups were estimated to be around four months old, and still dependent on their mothers (KIRKMAN & ARNOULD 2018). They do, however, frequently go to shallow waters for brief, independent exploration trips. Mothers also go on extended trips to sea to forage, which begins around four days after parturition (DAVID & RAND 1986).

Audio and video recordings of attraction calls produced by Cape fur seal pups and adult females were made. When an individual was seen returning from sea (visibly wet), either from foraging (mothers) or exploration (pups), a focal follow was initiated. Recordings of the focal individual were made from the first observed vocalisation until the animal would either stop vocalising for at least six minutes or move out of range of the recording device. Data were collected between 0800 hr and 1300 hr, after which the wind usually became too strong for clear recordings to be made.

All recordings were taken with a TASCAM DR-680M portable multitrack recorder (20 Hz to 20 kHz, +0.5/-0.5 dB) with a VP89L shotgun condenser microphone (40 Hz to 20 kHz, -33.5 dBV/Pa at 1 kHz) for focal recordings of the animals. The microphone was attached to a ~1.5 m telescoping boom and handheld to ensure on axis recordings of the focal individual. Recordings were made at a 48 kHz sampling rate, 24-bit, low gain, and +10 dB trim. A separate headset microphone was used by the researcher to record vocal notes *ad libitum*, identifying each time the focal animal vocalised. Videos were collected of each focal follow using a GoPro 4, which was mounted onto the boom to assist with confirmation of behavioural contexts where needed.

Animals were not marked, and only identified visually. Only recordings where the focal individual's identity was certain were used, e.g., if an animal was heard vocalising from behind a rock, but was not seen by the researcher, the recording would be discarded. By only recording animals seen returning from the sea we can ensure that each individual was recorded only once.

Data processing

Spectrograms of recordings (FFT length = 000, Hann window) were reviewed and annotated in Raven Pro 1.6 (Cornell Lab of Ornithology). All vocalisations for each of the focal animals were carefully selected, marking the start and end time of each individual vocalisation. Vocalisations were described by the age class (pup, adult female), vocalisation type and individual ID of the animal. All extracted vocalisations were used for comparative assessments of search effort and vocalisation length between the age groups, but focal follows that resulted in less than eight calls were excluded from analysis of percentage performance time and rhythmic patterns. The cut-off value was set at eight vocalisations to ensure that a bout is long enough to show basic patterning (e.g., beat or sub-pattern repetitions), while still including a sufficiently large sample of individuals for a meaningful analysis.

Data analysis

Total effort time (De) was calculated as the duration from the beginning of the first vocalisation to the end of the last vocalisation in a bout. Additionally, we calculated the duration of each individual vocalisation unit (Dvoc), and, if the animal vocalised at least eight times, the total time spent vocalising per total effort time (performance percentage time, Ppt; calculated as $\mathrm{Ppt} = \Sigma\mathrm{Dvoc} / \mathrm{De}$). We also calculated the total number of calls per individual and the duration of each inter-call interval (ICI; i.e., the silence between two successive vocalisations), and, for animals that vocalised at least eight times, the call rates as the number of calls per minute.

Calling effort

A one-way nested ANOVA was used to investigate call lengths as a response to age classes (adult female vs pup) with individual animals' ID used as the nested variable. A further ANOVA test was used to investigate the relationship between mean call duration and the total number of calls produced in a bout. Additionally, Wilcoxon-Mann-Whitney U tests were applied to check for significant differences between the ages classes in (1) the total number of vocalisations in a bout, (2) proportion of time spent vocalising within the effort time (Ppt), and (3) call rates (i.e., number of calls per minute). Investigating the effect of age class as a factor on calling effort was used to test the hypothesis that individuals that hold a higher stake in an event will expend more effort, such that during a mother and pup reunion unweaned pups will attempt a greater calling effort than mothers.

Temporal structure

A non-parametric Wilcoxon-Mann-Whitney U test was conducted to investigate differences in the ICIs between the two age classes (adult female vs pup). Additionally, temporal patterns were visualized by plotting (1) the calling patterns as event series, starting from the first vocalisation in a bout, and (2) histograms of time intervals between the onsets of each consecutive vocalisations in an individual's calling bout (inter-onset intervals, IOIs), with a 0.25s bin width. This method allows for an easy visual assessment of rhythmic patterning in event series and avoids unnecessary analyses if vocalisations prove to be non-periodic (RAVIGNANI & NORTON 2017; BURCHARDT & KNÖRNSCHILD 2020), or on the other hand, may indicate the appropriate in-depth analysis based on the rhythmic structure of the bout. Rhythmicity for individuals with at least eight calls was also evaluated using normalized Pairwise Variability Indices (nPVI) (GRABE & LOW 2002), which describe the temporal variability of a sequence, and can be used to identify patterns beyond the isochronous rhythm or clear sub-pattern repetitions, e.g., stress, syllable and mora timed structures (RAVIGNANI & NORTON 2017). Characterising rhythmicity could illustrate its role in encoding identity, an individual's attempt at anti-masking, or higher order structures in calling patterns.

Results

A total of 1137 FACs produced by 148 pups, and 439 PACs produced by 80 females were extracted After removing animals for which less than eight calls were recorded, our analysis of the intervals and rhythmic patterns of the calling bouts was narrowed to 824 FACs produced by 49 pups and 287 PACs produced by 20 adult females.

Calling effort

The mean length of PACs produced by adult females was 1.37 s (SD ±0.24), and that of FACs produced by young pups was 0.75 s (SD ±0.48) (Fig. 1).

There was a significant difference between call lengths in the two age groups, with females producing longer calls ($F_{(1,226)}=203.98$, $p<0.0001$). While a mixed effect model revealed significant individual differences ($p<0.0001$) in call lengths, the AIC selection (BURNHAM *et al.* 2010) proved that the age classes (AIC = -283.94) explained the differences in length better than individuality (AIC = 979.86). There was no relationship between the mean call duration and the total number of calls produced in a bout ($F_{(x,y)}=2.1157$, $p=0.1472$).

Pups produced significantly more calls during each bout than females ($W=7056.5$, $p=0.01608$). Pups produced a mean of 7.66 (SD ±7.82) calls per search, while females produced a mean of 5.69

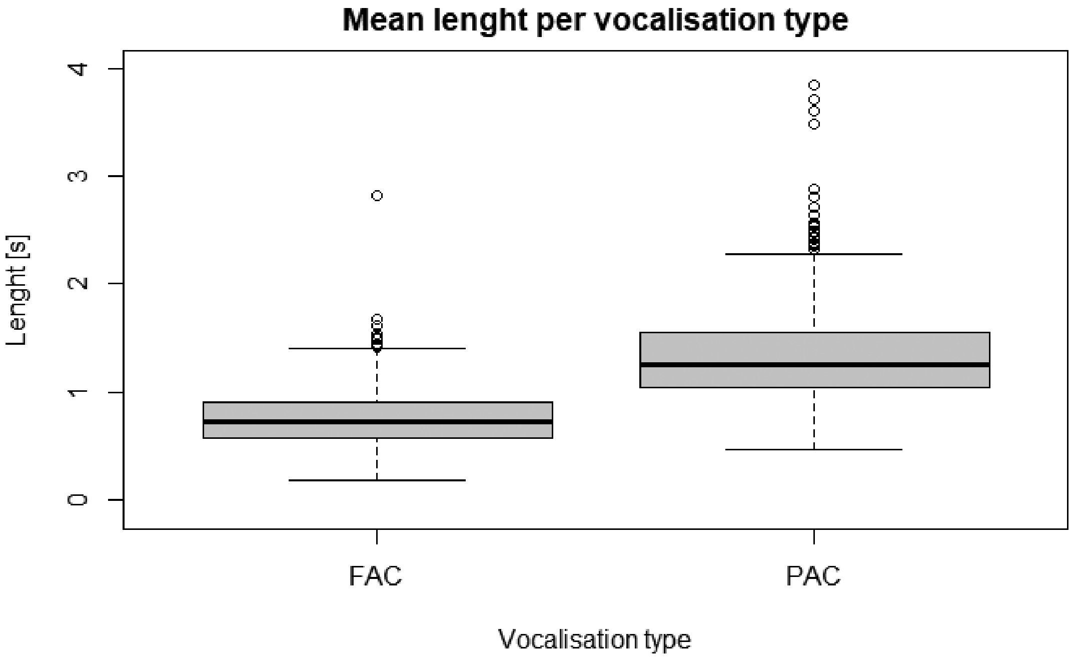

Figure 1 – Mean lengths of the attraction calls produced by pups (FAC) and females (PAC). The dark line represents the median/50th percentile; boxplots are delimited by the 25th and 75th percentile; whiskers end at the largest (upper) and smallest (bottom) value within 1.5 times the interquartile range above the 75th or below the 25th percentile.

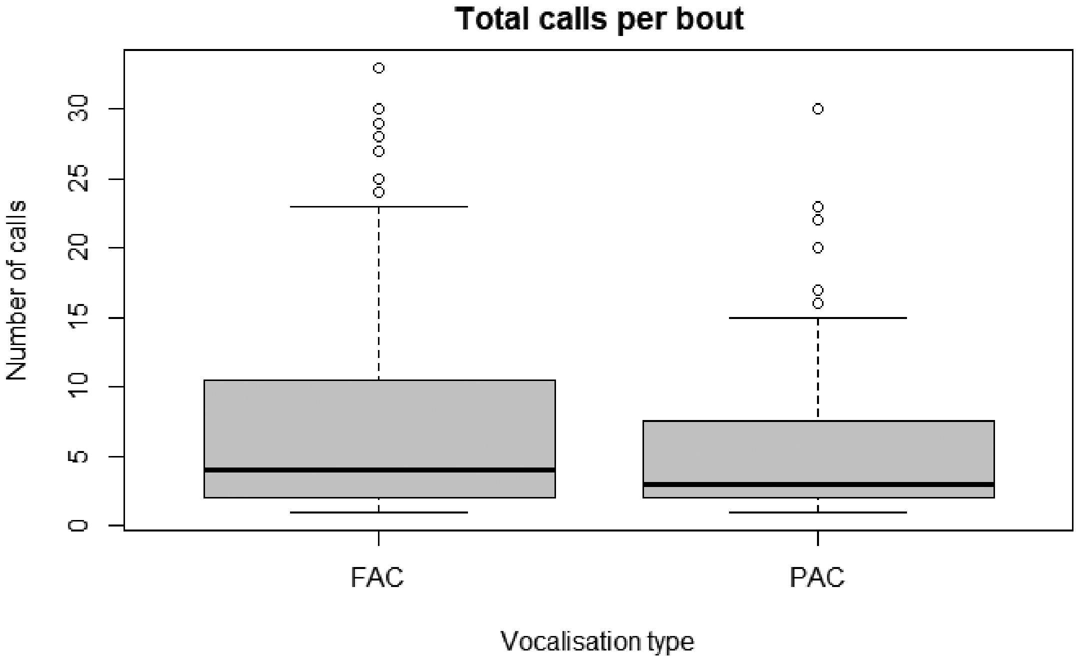

Figure 2 – Mean number of attraction calls produced in one vocalisation bout by pups (FAC) and females (PAC). The dark line represents the median/50th percentile; boxplots are delimited by the 25th and 75th percentile; whiskers end at the largest (upper) and smallest (bottom) value within 1.5 times the interquartile range above the 75th or below the 25th percentile.

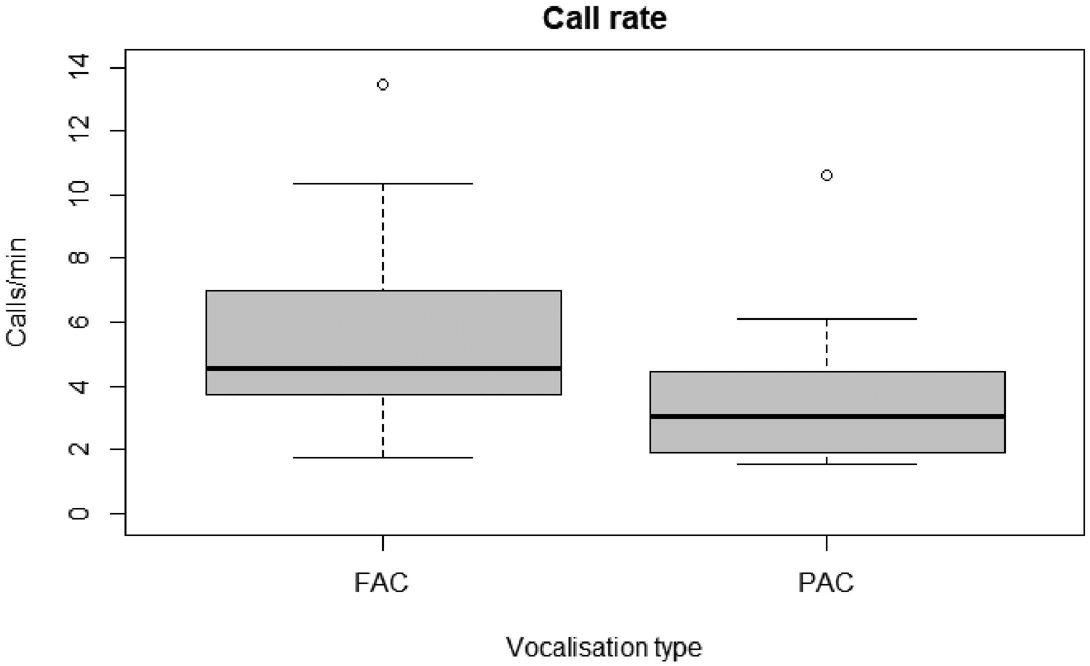

Figure 3 – Mean call rates of pups (FAC) and females (PAC), shown as the number of vocalisations per minute. The dark line represents the median/50th percentile; boxplots are delimited by the 25th and 75th percentile; whiskers end at the largest (upper) and smallest (bottom) value within 1.5 times the interquartile range above the 75th or below the 25th percentile.

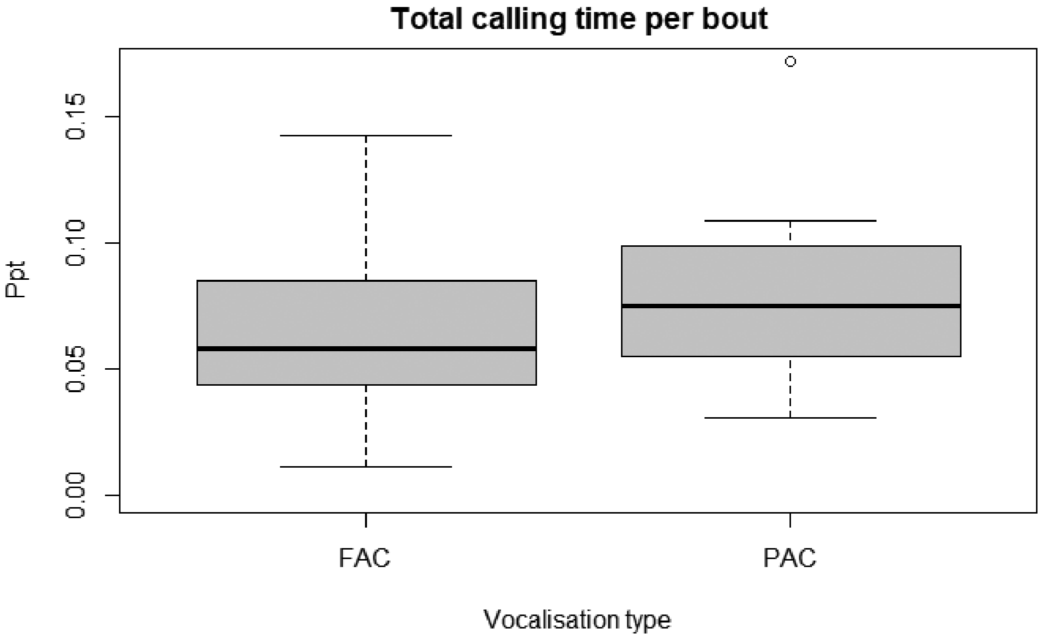

Figure 4 – Mean performance percentage time of pups (FAC) and females (PAC). The dark line represents the median/50th percentile; boxplots are delimited by the 25th and 75th percentile; whiskers end at the largest (upper) and smallest (bottom) value within 1.5 times the interquartile range above the 75th or below the 25th percentile.

(SD ±6.05) calls per search (Fig. 2). This resulted from the difference in calling rates, as the pups' calling bouts were typically shorter than the females' (mean pup bout=214.95s, SD ±117.87; mean female bout=296.68s, SD ±128.58). Call rates per minute were significantly higher for pups than for females (W=732, p=0.001088; FAC: mean=5.32, SD ±2.42; PAC: mean=3.54, SD ±2.13; Fig. 3). There was no significant difference between the percentage performance time of pups and females (W=366, p=0.1027; Fig. 4).

Temporal patterning

Females took significantly longer breaks between vocalisations (W=91451, p=0.004621; FAC: mean=12.79s, SD ±20.08; PAC: mean=20.69, SD ±34.47) although ICI's varied widely with several large outliers (FAC: ICI_{min}=0.28s, ICI_{max}=319.30s; PAC: ICI_{min}=0.72s, ICI_{max}=308.44s; Fig. 5). Plotted IOIs showed no stereotyped patterns, and were inconsistent both within and between individuals (see Figs 6–7 for examples and Appendix for additional individuals). Calculated nPVI for both FACs (mean nPVI=76.98, SD ±23.48) and PACs (mean nPVI=78.13, SD ±20.97) showed values midway between stress (where intervals between stresses are nearly equal; nPVI=92.74) and mora (where timing units are shorter than syllables; nPVI=52.84) patterns (GRABE & LOW 2002), suggesting complex asynchronous patterning.

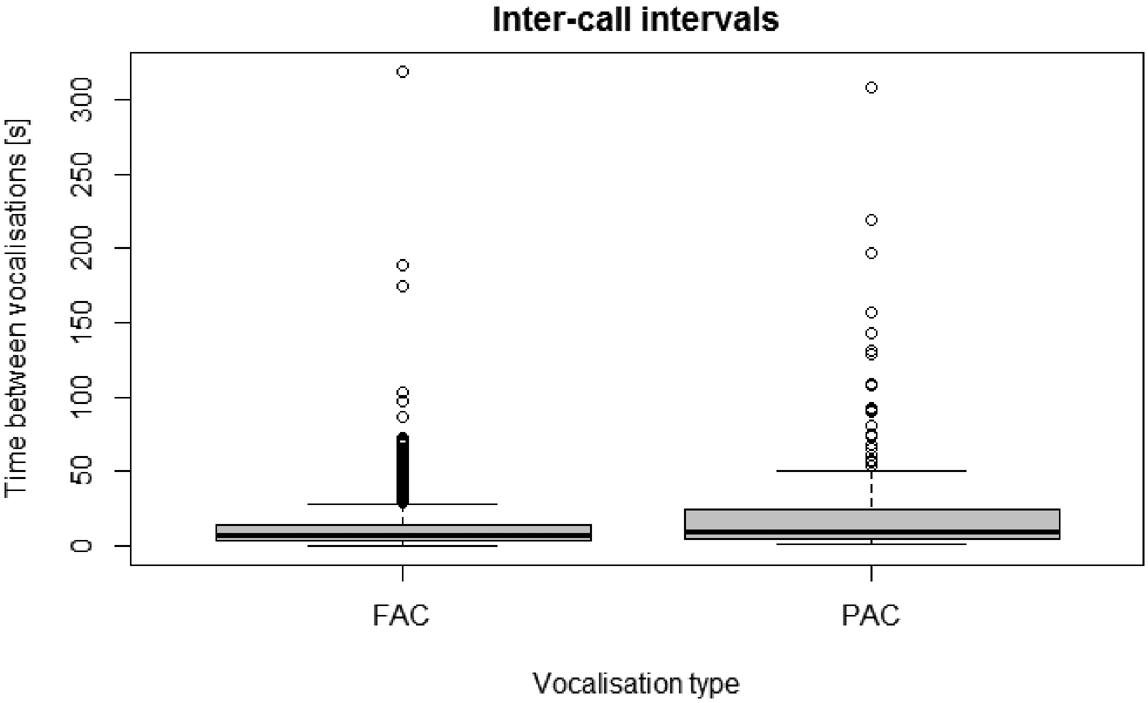

Figure 5 – Mean duration of silences between two consecutive calls produced by pups (FAC) and females (PAC). The dark line represents the median/50th percentile; boxplots are delimited by the 25th and 75th percentile; whiskers end at the largest (upper) and smallest (bottom) value within 1.5 times the interquartile range above the 75th or below the 25th percentile.

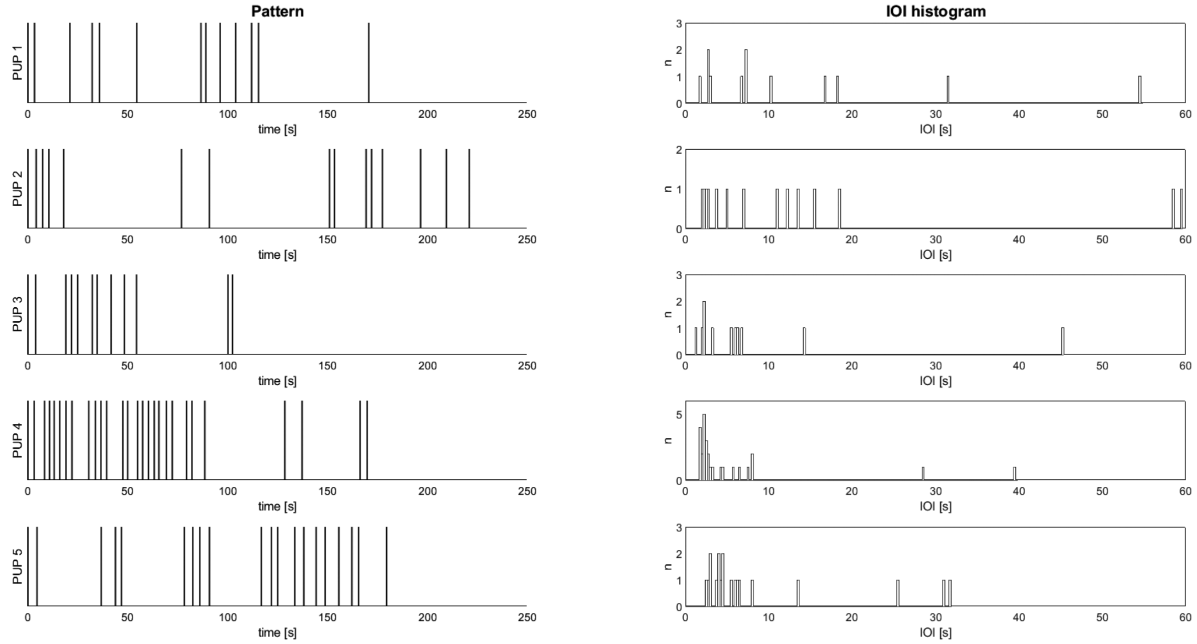

Figure 6 – An example of calling patterns (left) and histograms of their inter-onset intervals (right) for five different pups. All animals showed random call sequences.

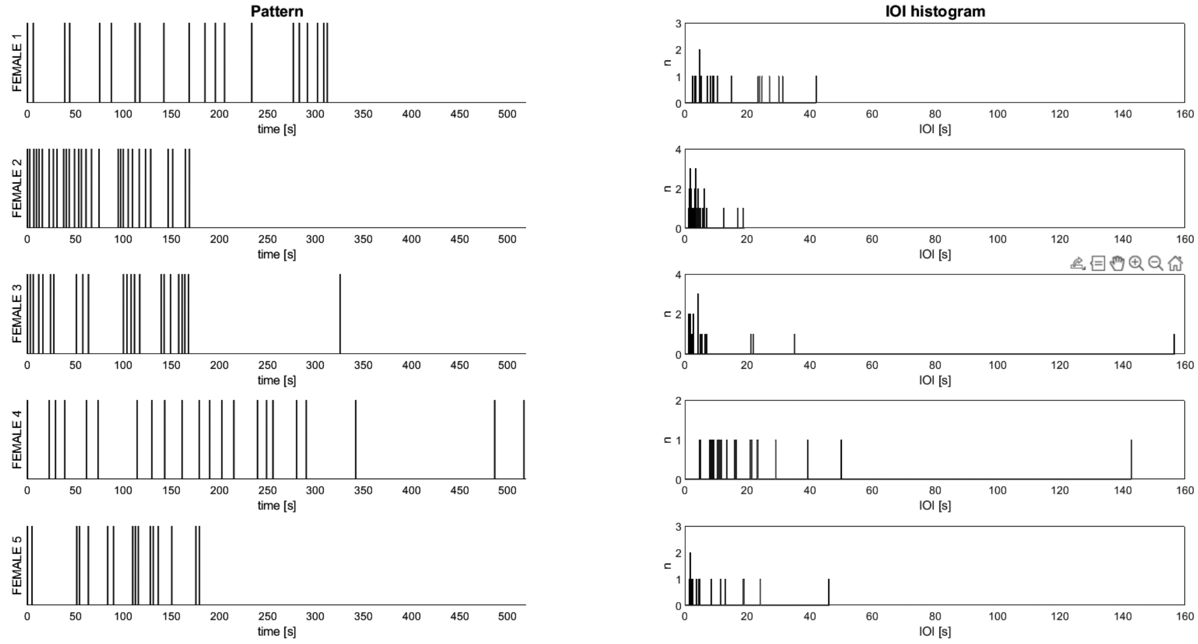

Figure 7 – An example of calling patterns (left) and histograms of their inter-onset intervals (right) for five different females. All animals showed random call sequences.

Discussion

Offspring survival is an important parameter to consider when assessing population dynamics. In colonial species of Otariids, pup mortality is causally related to the density of the colony (DOIDGE & CROXALL 1984). In Namibia, the mortality rate of the Cape fur seal of an age of up to 30 days is 20%, and likely caused from heat stress, starvation, or trampling (DE VILLIERS & ROUX 1992). Other populations of *Arctocephalus* have mortality rates for the first 300 days as high as 40%, with an increased cause from starvation (MATTLIN 1978). For an unweaned otariid pup, finding its mother upon her return from a foraging trip is a matter of life and death. At the same time, an active pup can often ensure a successful reunion upon its mother's return to the colony, independently of her behaviour (PHILLIPS 2003). It can thus be expected that the search effort will be higher from the side of the young.

Our study showed that Cape fur seal pups were significantly more active during the first observed vocal bout in a search than adult females: they produced a higher number of vocalisations, took shorter breaks between consecutive vocalisations, and vocalised at a higher rate per minute than females. These observations are comparable to temporal patterns observed in Northern fur seals, where both pups and mothers are vocal during a search, but pups significantly more so (INSLEY 2001). Nevertheless, attraction calls produced by the Cape fur pups were significantly shorter than those of females, and with lower vocalisation rates and longer inter-call intervals of the females, the proportion of time spent vocalising during a bout was similar for mothers and pups.

It is possible that the longer inter-call intervals and lower call rates of females are not completely dictated by lower motivation, but rather by physical constraints. A lactating female is under intense physiological stress (OFTEDAL & GITTLEMAN 1989), which for Cape fur seal mothers can extend beyond the usual one year (KIRKMAN & ARNOULD 2018; OSIECKA *et al.* 2020). Since female vocalisations are much longer, it may become exhausting or physically impossible to keep vocalisation rates equal to those of pups, as a longer break is necessary to recover after a longer vocalisation. We propose that the relative energy expenditure during the initial phases of search efforts is comparable for pups and mothers in Cape fur seals. This, however, may not necessarily translate directly into the real energetic cost of an individual. Expending equal amounts of energy may have a larger effect on a small pup than it does on an adult female up to ten times its weight (WARNEKE & SHAUGHNESSY 1985), even during lactation.

Vocalising can be energetically costly (e.g., MCCARTY 1996; DEECKE *et al.* 2005; HOLT *et al.* 2015), particularly when signalling an urgent need or when in distress (WEARY & FRASER 1995). Higher vocalisation rates can often be associated with a more intense emotional expression (BRIEFER 2012; MARTIN *et al.* 2022) or motivational state of the animal (e.g., PITCHER *et al.* 2014; FERNÁNDEZ-VARGAS & JOHNSTON 2015; CUSANO *et al.* 2020). For example, a female might produce calls at higher rates when returning from a longer foraging expedition, than if she was absent for a shorter amount of time, i.e., when her young is in greater need of food. Motivation may also change at different stages of the search effort (COLLINS *et al.* 2011). For example, a pup might call more often if it becomes increasingly hungry or may be triggered into higher call production rates after hearing a pup attraction call produced by its mother or another female, as observed in the Northern fur seal (INSLEY 2001) and the Weddell seal (*Leptonychotes weddellii;* COLLINS *et al.* 2011). It seems plausible that a similar relationship would exist for the Cape fur seal. Since our study was purely observational and did not include marking, tagging, or experimental control of stress levels, it was impossible to know exactly how long the females had been absent upon their return. Therefore, we cannot make conclusions about how call rates and temporal patterns may vary between different motivation states, or possible vocal expression of emotions in the Cape fur seal. Future studies including tagging mother and pup pairs with equipment collecting both GPS data and audio recordings would be useful to understand the interplay between the length of separation and vocal efforts of the mother-pup pair. Similarly, additional controlled observations would be necessary to understand how such patterns may vary between finer age classes of the seals.

Highly rhythmic vocalisations convey information on identity (Sanvito & Galimberti 2000; Sanvito *et al.* 2007; Mathevon *et al.* 2017) and behavioural contexts (Schusterman 1977; Tripovich *et al.* 2008; Martin *et al.* 2022) in some pinniped species. We did not find any stereotyped rhythmic patterning in the attraction calls of Cape fur seal pups nor females. Upon visual inspection, the animals seemed to vocalise at random intervals, inconsistent at both the individual or population level. Vocalisation bouts seem to be divided by longer periods of silence, used possibly to rest and/or listen, yet such silences do not impact the overall interval frequency. This suggests that no additional stereotyped identity information is coded in the calls' rhythmic structure.

However, the rhythmic pattern of a vocalisation series, or bout, does not necessarily have a meaning on its own but can instead hide more complex communication systems (Kershenbaum *et al.* 2016). Pups of some phocids seem to time their asynchronous calls and adjust calling rates to avoid masking (Ravignani 2019; De Heer Kloots *et al.* 2020) in such a way to avoid coincidence with predictable noise (Ravignani 2019) or other pups (De Heer Kloots *et al.* 2020). Though a similar mechanism would be impossible in the crowded otariid colonies, and indeed attraction calls produced by Cape fur seal pups often overlap (personal observations), the existence of such a mechanism cannot be excluded without experimental trials. A more thorough exploration of rhythmicity (nPVI) did in fact indicate potential asynchronous patterning, suggesting a speech-like complexity – that is, the temporal variability of sequences was estimated as closer to stress or mora rhythms described in human languages, than to random sequencing (Grabe & Low 2002). Information could be encoded in asynchronous syllabic stressors, possibly representative of the animals' emotional state, motivation, or as a way to limit masking. Dedicated investigations into rhythmic patterns and how they change over the duration of an entire search effort (from onset to reunification of pups and mothers), would be necessary to understand these effects and possible inter-individual patterning.

Additional cues might facilitate mother-and-pup reunions and recognition. For example, females of Australian sea lions (*Neophoca cinerea*) use body size and colour pattern to distinguish different age-classes of the young (Wierucka *et al.* 2017). However, such visual recognition is likely limited to short distances, since in air pinnipeds are myopic (Wartzok & Ketten 1999). Few descriptions of the use of spatial cues by other Otariids exist, such as memorising the area of the colony where the pup was left (Phillips 2003; Trimble & Insley 2010), which could be helpful at larger distances. If similar mechanisms are used by the Cape fur seals, they could narrow the search areas within their colonies which can host up to hundreds of thousands of individuals (Kirkman *et al.* 2013). Finally, Otariids show extreme levels of vocal individuality, related to the colony densities (Trimble & Charrier 2011; Martin *et al.* 2021b) and coded entirely at the level of a single vocalisation (e.g., Charrier *et al.* 2002, 2003; Charrier & Harcourt 2006; Trimble & Charrier 2011; Martin *et al.* 2021b).

The apparent lack of stereotyped rhythmic patterning suggests that other cues, such as strong vocal individuality or memorisation of preferred spatial locations, may be used in reunions. There is however a potential for a more complex asynchronous patterning, calling for further investigations of rhythmicity in pinniped communication.

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Animal welfare concerns

This work was based of passive observations only, and caused no disturbance nor harm to the animals.

Authors' contributions

Authors declare no conflict of interest. AO and TG designed the study. AO and JF collected, processed, and analysed the data. AO prepared the first manuscript. All authors contributed to the interpretation and writing of this work.

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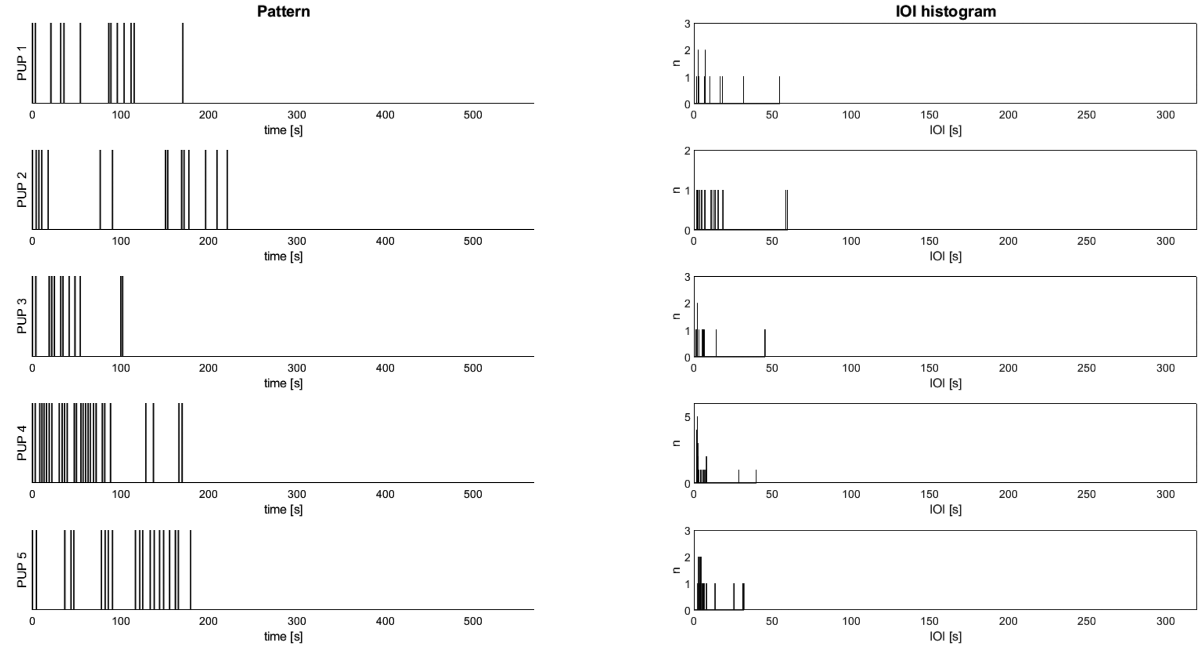
Appendix

Calling patterns (left) and histograms of their inter-onset intervals (right) for additional pups (Supplementary Figures 1–10) and adult females (Supplementary Figures 11–14).



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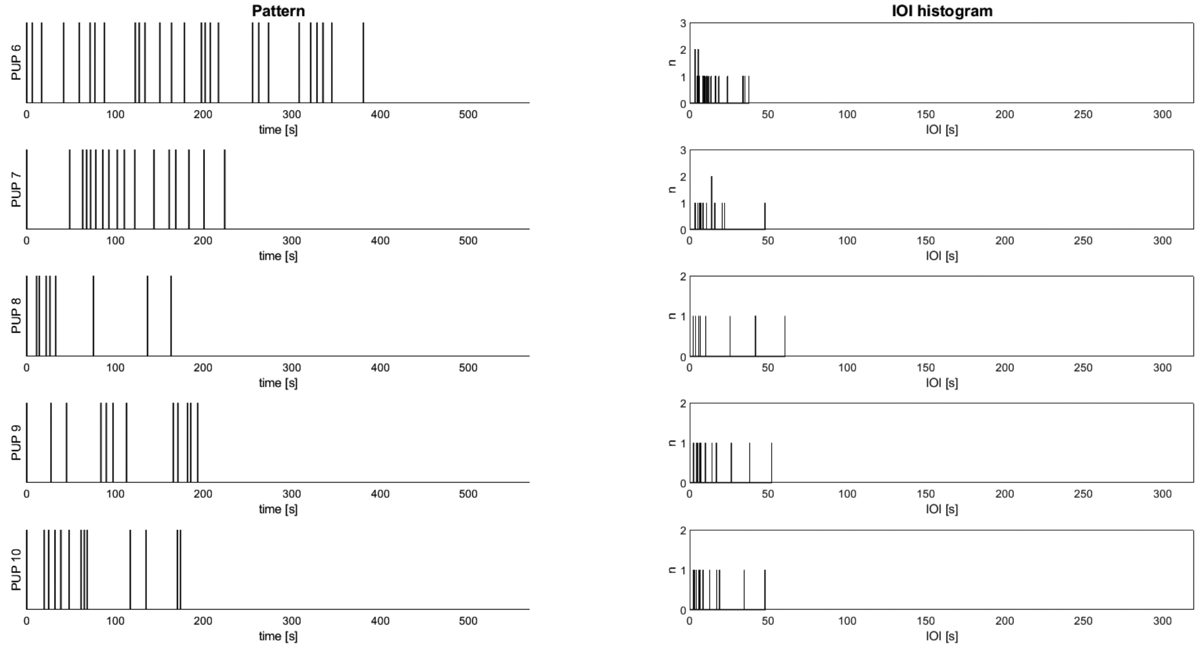

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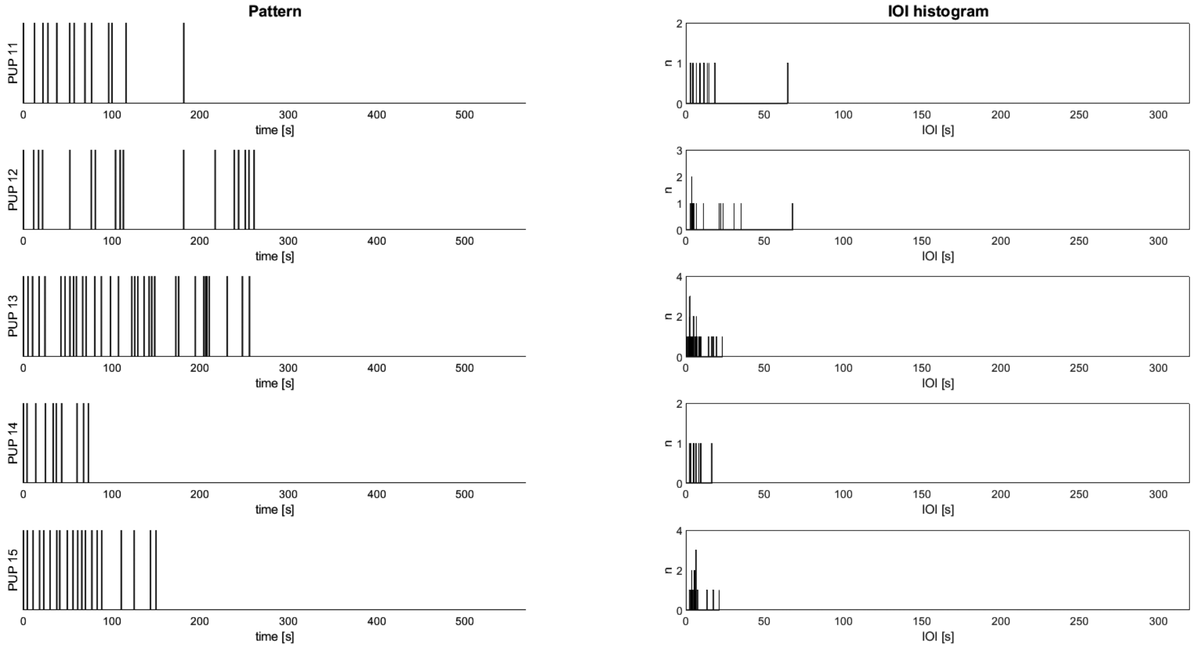

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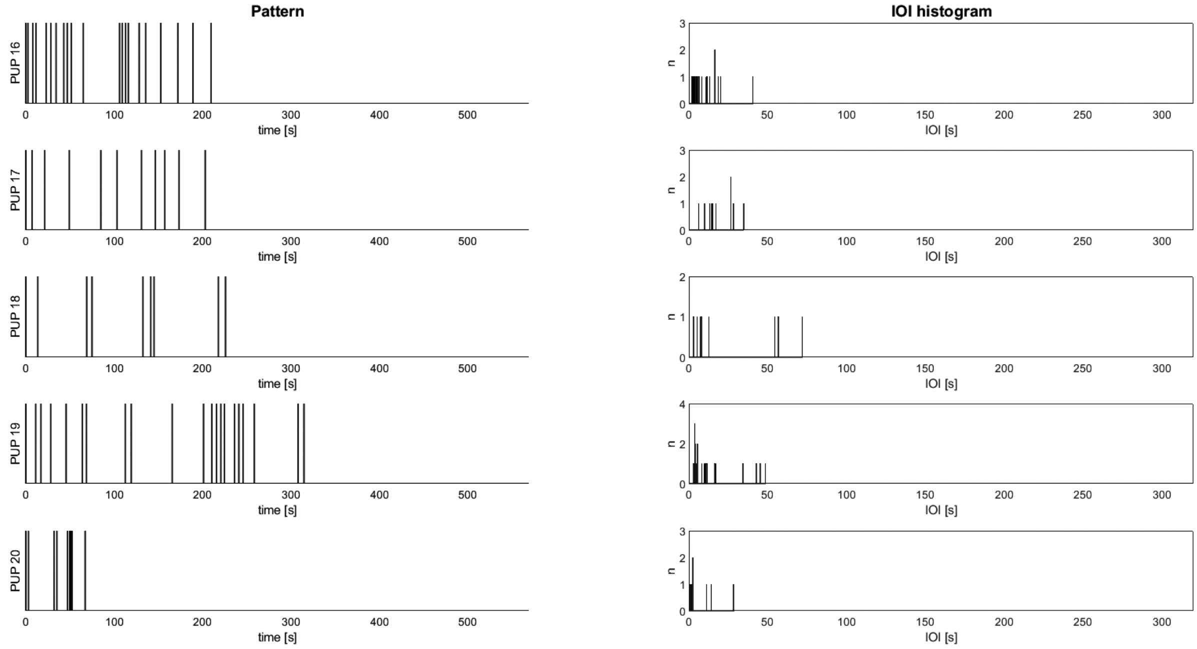

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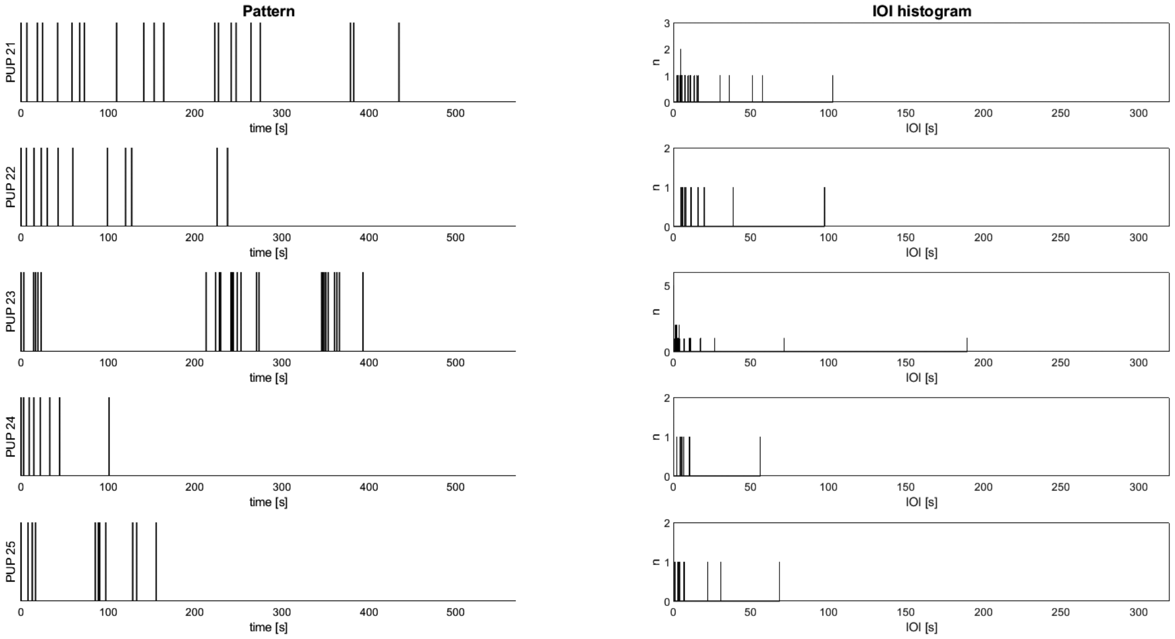

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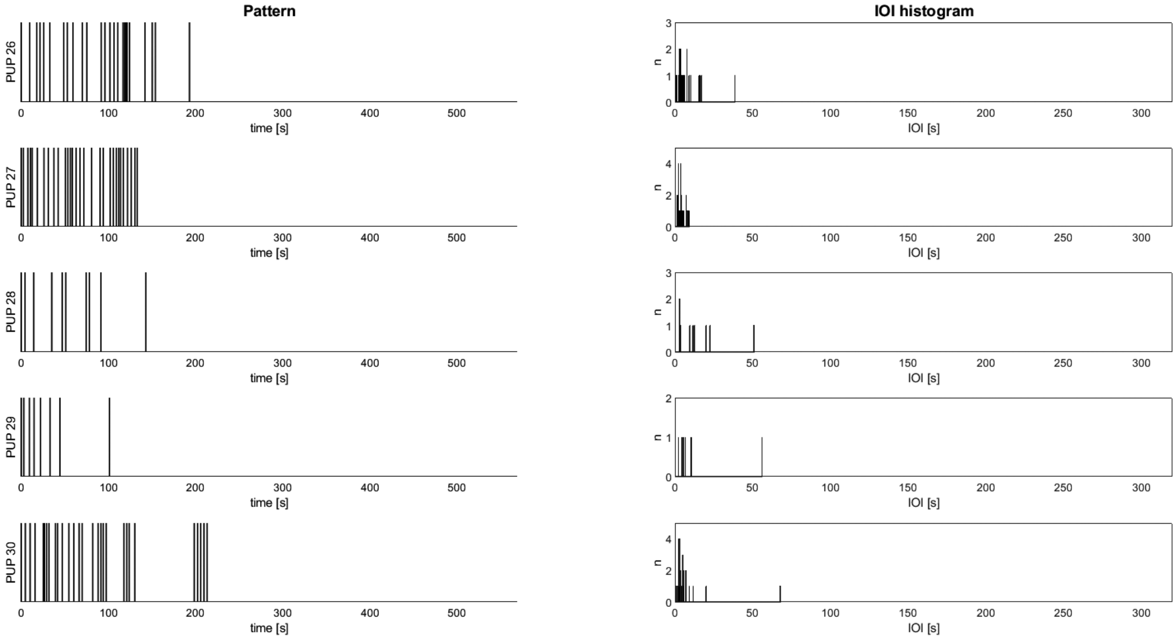

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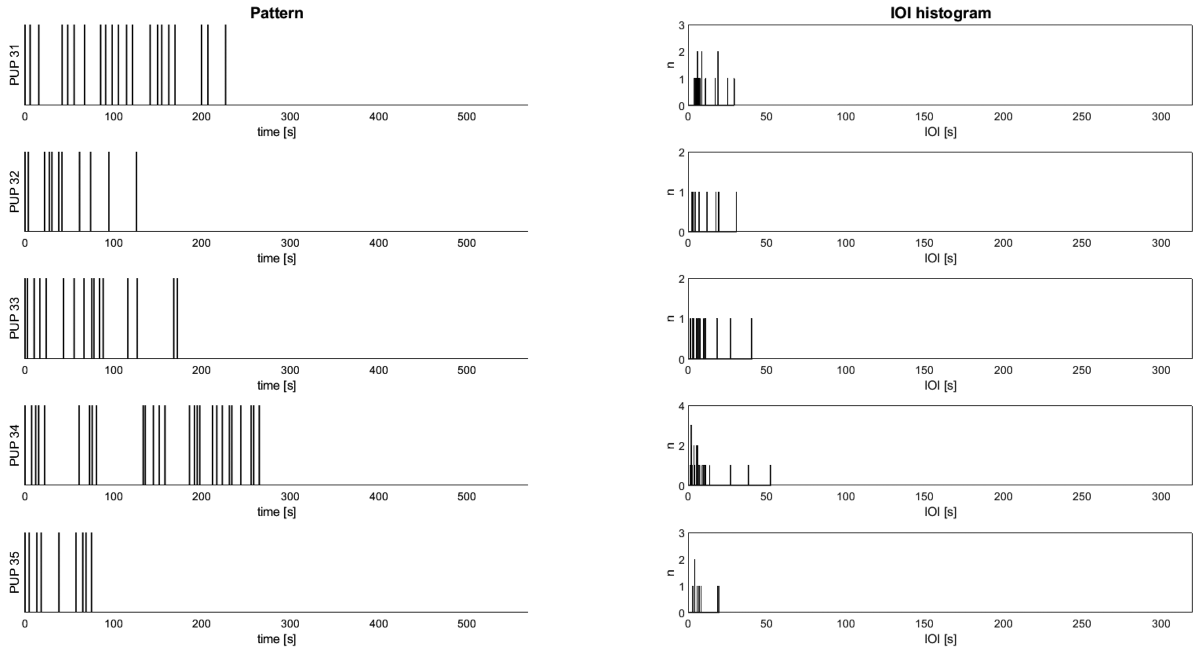

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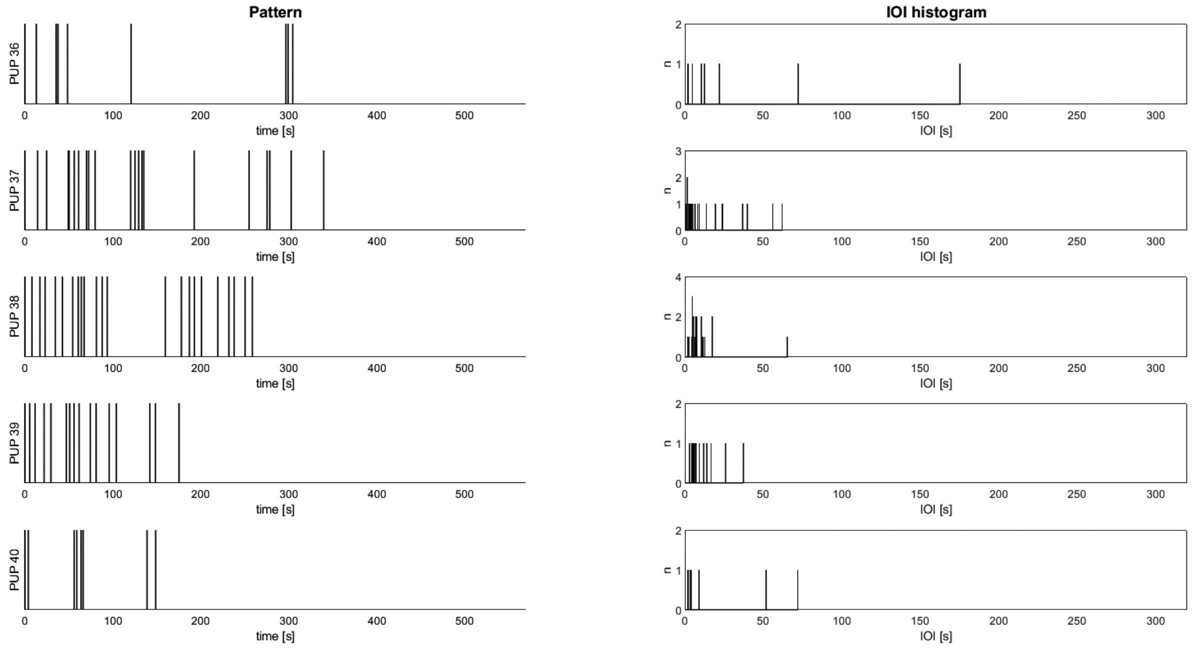

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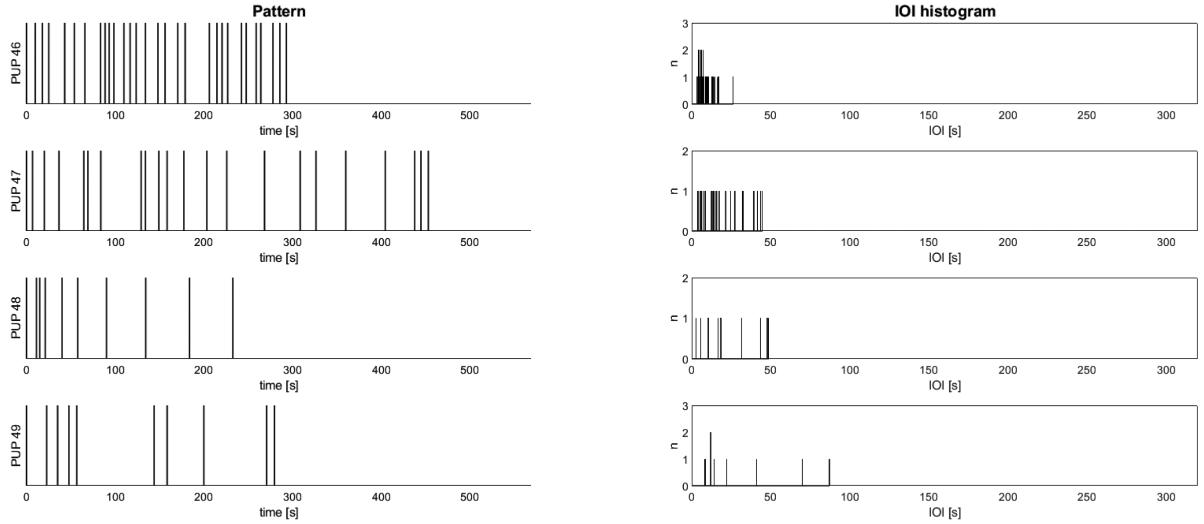

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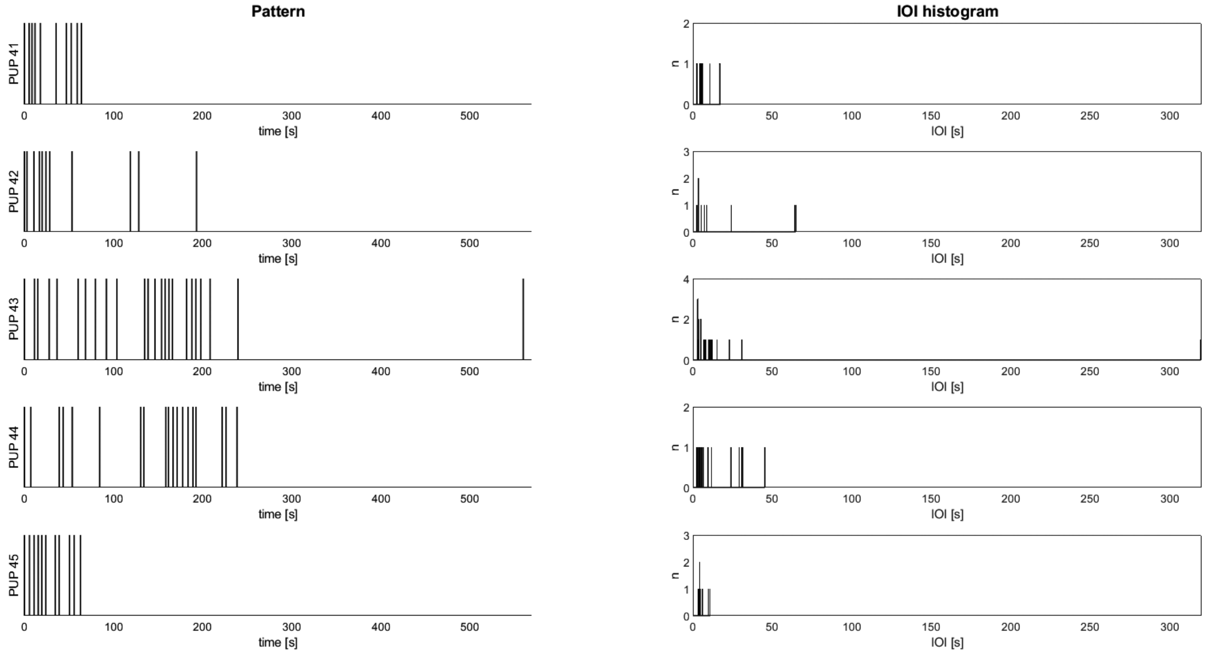

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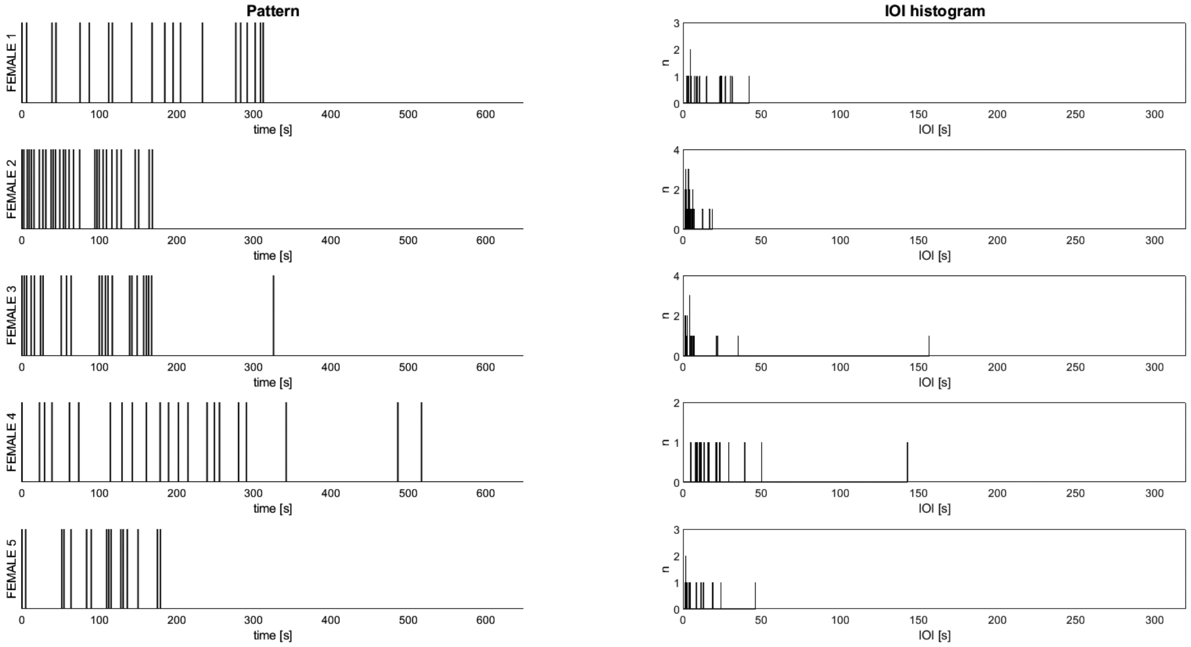

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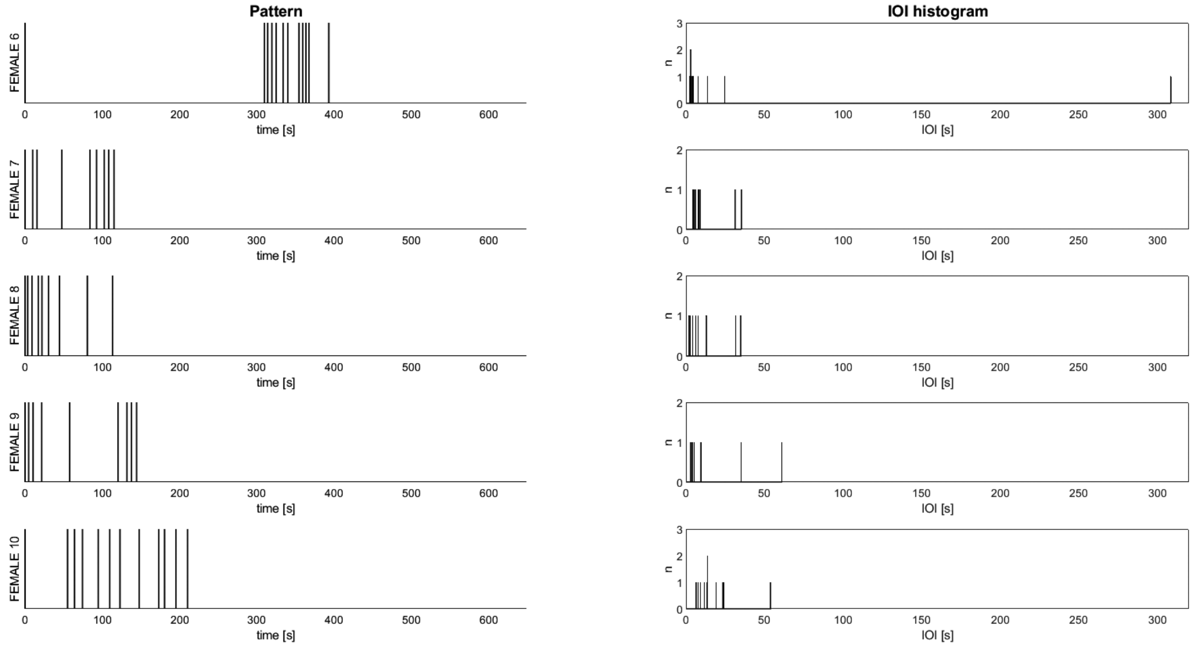

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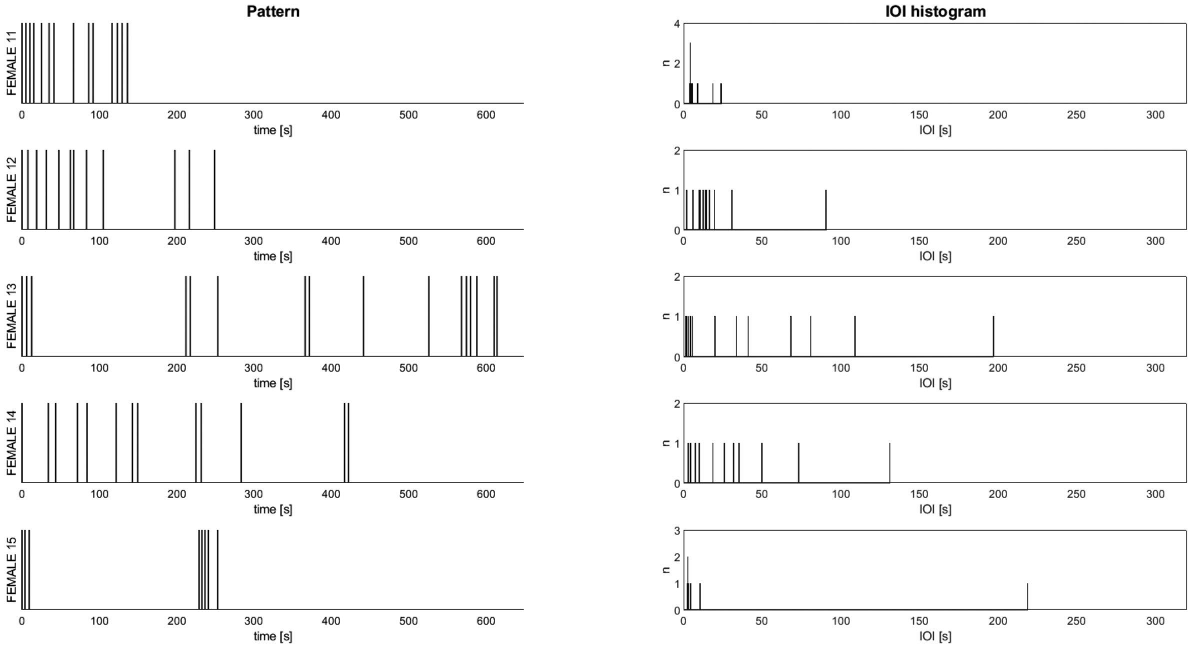

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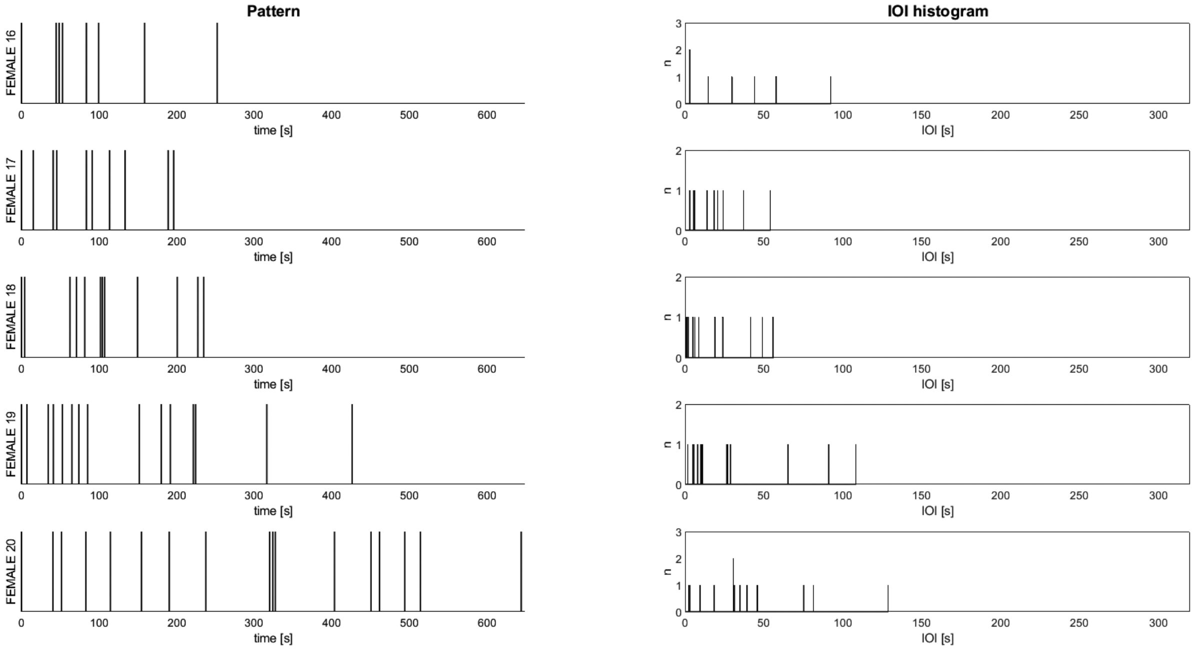

Supplementary Figure 14.