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Measuring rhythms of vocal interactions: A proof of principle in harbour seal pups

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3 **Author-supplied statements**
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5 Relevant information will appear here if provided.
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8 **Ethics**
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10 *Does your article include research that required ethical approval or permits?:*

11 Yes
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13 *Statement (if applicable):*

14 This research was conducted following the principles of animal care and the Dutch and EU
15 regulations for the ethical treatment of animals in behavioural research and was subject to the
16 health and needs of the animals. All recordings complied with the guidelines outlined by the
17 Veterinary Department of the Sealcentre Pieterburen.
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23 *available. Does your paper present new data?:*

24 Yes
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27 The datasets and codes for statistical analysis used in this article have been uploaded as part of the
28 Supplementary Material. Please follow this link to find the related files:
29 https://osf.io/8m4yv/?view_only=2549b6002bbc4dbd9a86735a7e8393d0
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Measuring rhythms of vocal interactions: A proof of principle in harbour seal pups

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Abstract

Rhythmic patterns in interactive contexts characterise human behaviours such as conversational turn-taking. These timed patterns are also present in other animals, and often described as rhythm. Understanding fine-grained temporal adjustments in interaction requires complementary quantitative methodologies. Here, we showcase how vocal interactive rhythmicity in a non-human animal can be quantified using a multi-method approach. We record vocal interactions in harbour seal pups (*Phoca vitulina*) under controlled conditions. We analyse these data by combining analytical approaches, namely categorical rhythm analysis, circular statistics, and time series analyses. We test whether pups' vocal rhythmicity varies across behavioural contexts depending on the absence or presence of a calling partner. Four research questions illustrate which analytical approaches are complementary vs. orthogonal. For our data, circular statistics and categorical rhythms suggest that a calling partner affects a pup's call timing. Granger causality suggests that pups predictively adjust their call timing when interacting with a real partner. Lastly, the ADaptation and Anticipation Model (ADAM) estimates statistical parameters for a potential mechanism of temporal adaptation and anticipation. Our analytical complementary approach constitutes a proof of concept; it shows feasibility in applying typically unrelated techniques to seals to quantify vocal rhythmic interactivity across behavioural contexts.

Keywords: Behavioural interaction, asynchrony, circular statistics, categorical rhythms, time series analysis, interactive vocal rhythm

1. Introduction & methodological approaches

1.1. Rhythmic interaction and turn-taking

Humans adopt precise signalling behaviours to exchange information [1,2]. No matter the signal modality (e.g., acoustic, visual), an interactive event between sender and receiver is governed by a timed structure [3–6]. The structured exchange of communicative turns (i.e., turn taking) characterises our capacity for social interaction, enabling us to communicate with others [7,8]. The study of interactive rhythms—how two (or more) individuals coordinate their signalling in time—is an emerging field of research, with more recent work extending structural analyses of communication signals, once restricted to human spoken conversation, to other species [3,9]. Turn-taking in communication has been documented in primates [10] and in other non-primate species [6,11–13]. For example, call exchanges in adult common marmoset monkeys (*Callithrix jacchus*) exhibit coupled oscillator dynamics, like those observed in human turn-taking [14]. Two key components of turn-taking are the flexible organisation and distribution of turns, and the temporal relationship between adjacent turns [11]. In humans, face-to-face interactions require participants to be, among others, both socially and temporally sensitive [15]. Does behavioural context also affect signal timing in non-human animals? Comparative investigations on interactive vocal timing in mammals may help uncover shared turn-taking mechanisms, potentially providing more insights into their evolution.

1.2. Methodological approaches and challenges for studying rhythmic interaction

Expanding the human turn-taking framework to other species is currently hindered by, among other things, lack of suitable methodological approaches [11,16]. Cross-species frameworks exist [17], but open questions still remain in animal face-to-face interaction, such as: Which analytical methodologies used to investigate turn-taking in humans may reveal temporal adjustments in other species? Can turn-taking arise from non-cooperative behavioural interactions? Can methods developed for individual rhythm analyses be used to study rhythmic interaction? Can parametric models for human rhythmic prediction and reaction detect similar features in other species? These open questions require suitable animal models and quantitative methods.

Different forms of vocal rhythmic interaction, such as synchronous chorusing and turn-taking, have been mainly studied in mammals within a cooperative dynamic, like parent-infant and male-female dyads. Time series analyses like Granger causality have shown temporal interdependence between vocalisations in male-female pairs [18,19] and movements [20] of non-human primates. Circular statistics is another method to study timing adjustments in interactions, and has been used in previous animal work, including a seal pup playback experiment [21] and a study on parent-infant monkey interaction [22]. Categorical rhythms—those for which the temporal intervals between signal onsets are distributed categorically rather than uniformly—are a universal characteristic of human

1
2 90 music, which is often produced in an interactive context [23]. Similar rhythms are also present in non-
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4 91 human animal songs (e.g., thrush nightingales [23], indris [24], but whether such rhythms characterise
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6 92 other interactive non-song vocalisations, such as animal calls, is unknown [23,24]. Roeske and
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8 93 colleagues [23] hypothesised that categorical rhythms play a role in calls produced to attract and hold
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10 94 conspecific attention, by making sequences of vocalisations more predictable to listeners. Categorical
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12 95 rhythm analyses could therefore be an interesting method to test the predictability of vocal sequences
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14 96 in non-human animal interactions. Lastly, the ADaptation and Anticipation Model (ADAM),
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16 97 originally developed to model the mechanisms for interpersonal coordination in humans [25], has
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18 98 been adopted to probe sensorimotor and cognitive mechanisms underlying temporal dynamics in
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20 99 interaction [26,27]. Although ADAM is designed for ‘simultaneous chorusing’, it could also be used
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101 for a mixture of bouts of synchrony, turn-taking, and other regimes [21,28].

21 101 In this proof of concept study, we showcase how these methodological tools— Granger
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23 102 causality, circular statistics, categorical rhythm analysis, and ADAM—can be applied to a new animal
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25 103 model: the harbour seal (*Phoca vitulina*). To illustrate the utility and compatibility of these different
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27 104 analytical methods, we show how they can be used to better understand the rhythmic communication
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29 105 of a small sample of harbour seal pups in different behavioural contexts.

30 106 31 107 **1.3. Our animal model**

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33 108 The “vocal learning-beat perception and synchronisation” (VL-BPS) hypothesis states that only
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35 109 vocal learning species—those capable of producing new vocalisations or modifying existing ones
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37 110 based on auditory experience—may possess advanced rhythmic abilities [29,30]. This hypothesis is
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39 111 inherently cross-modal: it suggests a strong link between audition and timed movement. For example,
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41 112 Snowball, a sulphur-crested cockatoo (*Cacatua galerita eleonora*), was shown to perceive auditory
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43 113 rhythms at different tempi and to predictively synchronise his body movements to them [31]. Parrots
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45 114 are phylogenetically distant from humans and, among mammals, pinnipeds (seals, sea lions, and
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47 115 walrus) are one of the vocal learning groups (besides humans, bats, elephants, and cetaceans).
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49 116 Pinnipeds may well be the best mammalian model for testing the VL-BPS hypothesis—the ability to
50
51 117 extract a beat from periodic acoustic stimuli and entrain to it in a predictive and adaptive manner—
52
53 118 since some species showed vocal mimicry and plasticity [32,33] and others can keep a beat [34].
54
55 119 These characteristics, paralleling human abilities, make pinnipeds an ideal animal clade for
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57 120 comparative research on the origins of rhythmic communicative behaviour.

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59 121 Harbour seals exhibit both vocal flexibility [33,35] and rhythmic interactivity [21], and are
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122 particularly vocal in the first few weeks of life [36]. During the lactation period, harbour seal pups
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124 emit ‘mother attraction calls’ (hereafter ‘calls’) to draw their mothers’ attention [37]. Mothers are
silent and use the individual vocal signatures in these calls to recognize their pups [36,38]. Against

1
2 125 the acoustically complex backdrop of large mother-pup rookeries, rhythmically tuned pup calls could
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4 126 constitute a socio-ecologically selected trait that allows individual pups to avoid conspecific call
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6 127 overlap by adjusting the timing of their own call onsets. Such timing plasticity could allow a pup to
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8 128 be more acoustically conspicuous and increase its chances of successful reunions with its mother.
9 129 Unlike cooperative types of turn-taking (e.g., in humans and in common marmosets (*Callithrix*
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11 130 *jacchus*) [39]) harbour seal pups' interactions are a by-product of neighbouring pups vocalising to
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13 131 attract their silent mothers, and are thus probably competitive.

14 132 To date, only two papers studied vocal rhythms in harbour seals, crucially both focusing on
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16 133 single individuals [21,28]. The first study was a playback experiment in which a pup vocally
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18 134 interacted with sounds broadcasted from a loudspeaker [21]. The pup adjusted the timing of its calls
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20 135 in an asynchronous manner by responding to the broadcasted conspecific calls with a non-uniformly
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22 136 distributed response phase whose mean approximated 90° [21]. The second study looked at the
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24 137 presence and development of vocal rhythms in three harbour seal pups [28]. Complementary
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26 138 analytical approaches showed how the pups' *individual* calling patterns gained more rhythmic
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28 139 structure over time [28]. However, a major limitation of both studies was the lack of sociality (i.e.,
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30 140 individuals were tested alone) and, by extension, interactivity (i.e., the stimuli did not adapt to the
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32 141 response of the tested animals).

33 143 **1.4. Aims & research questions**

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35 144 In this work, we show how vocal interactive rhythmicity in non-human animals can be
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37 145 quantified using a multi-method approach spanning various research domains (e.g., temporal, social,
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39 146 cognitive) (Table 1). We illustrate this approach through four research questions, all of which relate
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41 147 back to whether harbour seal vocal interactive rhythmicity varies in different behavioural contexts
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43 148 (Table 1). While our sample sizes are too small to enable species-wide inferences, they are sufficient
44
45 149 to illustrate how methods typically used to study human communication can be adopted to study
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47 150 interactivity in animal communication. The goal of this paper is thus to outline a quantitative roadmap
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49 151 that future research can follow. Circular statistics and categorical rhythm analysis are used to address
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51 152 the first question about temporal adjustment in interaction: “*does the presence of a calling partner*
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53 153 *affect the call timing of individual pups?*” (Q1). The next two questions consider the effect of
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55 154 behavioural context on temporal adjustment: “*does the type of calling partner (real or broadcasted)*
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57 155 *affect the call timing of individual pups?*” (Q2) and “*when the focal pup is vocalising, does the*
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59 156 *presence of a silent partner (vs. no partner) affect call timing?*” (Q3). We answer these questions
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157 using circular statistics (Q2 and Q3) and Granger causality tests (Q2). Lastly, ADAM is used to
158 investigate the fourth question about the cognitive processes involved in temporal adjustment: “*which*
159 *timing mechanisms are used by pups during vocal interactions?*” (Q4).

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4 161 **1.5. Subjects, housing conditions, and behavioural contexts**

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We recorded nine wild-born pups (A-I) calling in different behavioural contexts while housed at Sealcentre Pieterburen (the Netherlands) (Method S1/S2). During the recordings, each pup was housed in an enclosure with a swimming pool and a resting platform (Figure S1). One pup was housed alone (I) while the others were housed in pairs (A/B, C/D, E/F, G/H). Note that the enclosures were physically but not acoustically isolated from each other, meaning that pups could hear other pups in neighbouring enclosures.

We analysed focal pup vocalisations during four different behavioural contexts (Figures 1, Table S1): (i) when the focal pup was alone (pup I), (ii) when the focal pup heard a playback of conspecific calls (pup I), (iii) when the focal pup's partner was silent (pups A-H), and (iv) when the focal pup's partner was also vocalising (pups A-H). Hereafter, we refer to these conditions as: (i) alone, (ii) 1-way interaction with a broadcasted partner, (iii) silent partner, and (iv) 2-way interaction with a real partner. Notice that only some pups entered each condition and vice-versa (Table S1).

Our sample size was affected by the unpredictable arrival of animals at the Sealcentre, which varies seasonally. Only medically stable and healthy pups were included in this study. The number of daily recording sessions per pup pair varied based on veterinary staff recommendations at the rehabilitation centre (Table S1); we did not record pups with signs of disease. Data from pup I (i.e., the alone and 1-way contexts both with and without playback stimuli) have been re-analysed from previous studies [28,21, respectively] and combined with unpublished data from pups A-H (the silent partner and 2-way contexts) (Table S1). The contribution of each pup to each analysis is shown in Table S2.

42 183 **1.6. Extraction of temporal variables, definition of call bout and vocal interactions**

We first extracted the onsets and offsets of each pup call recorded in each behavioural context (Figure 1, Method S3). From these values, we calculated rhythmic metrics such as call duration, inter-onset intervals (IOIs), ratios of adjacent IOIs, and inter-call intervals (ICIs; i.e., silent gaps). Each IOI was obtained by subtracting the *onset* of call n from the *onset* of call $n+1$, while the ICI was calculated by subtracting the *offset* of call n from the *onset* of call $n+1$ (i.e., IOI minus duration of call n). Calls were organised into bouts, defined here as a series of at least three subsequent calls that were separated from adjacent bouts by a period greater than 1.5 times the median ICI of the recorded individual(s) calls (Figure 1). The response phase was computed as the ratio of the 'response IOI' (i.e., time interval between the call onset of the partner and the call onset of the pup's response) and the previous IOI, multiplied by 360, resulting in a unit vector with an angle on a circle. A vocal interaction was defined as a group of three calls within the same bout, which includes two calls from the broadcasted/real

partner followed by the response of the focal individual (Figure 1). Following previous methodology [28,38], we calculated the IOI ratio, r_k , for each pair of adjacent IOIs, t_k and t_{k+1} , in a bout as:

$$r_k = \frac{t_k}{t_k + t_{k+1}}$$

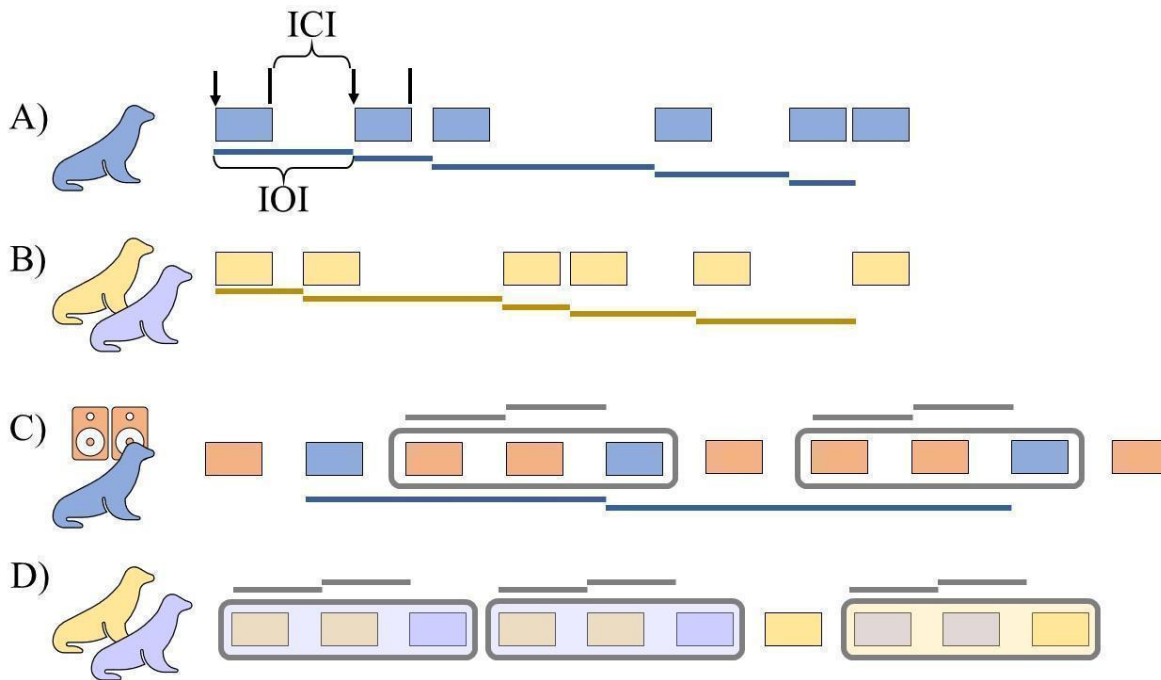


Figure 1. Schematic of experimental conditions and key measurements. Each of the four rows represents one bout and indicates a different behavioural context: (A) alone, (B) silent partner, (C) 1-way interaction, and (D) 2-way interaction. Boxes are coloured to represent the call source and grey rectangles denote vocal interactions. For bouts (C) and (D), calls are isochronously spaced for ease of visualisation, but empirical patterns were not necessarily isochronous. Horizontal bars indicate how IOIs were calculated for different analyses. The call onsets (black arrows) and offsets (black lines) are shown for the first two calls in (A).

1.7. Descriptions of analytical approaches

Circular statistics, wherein periodic measures are converted to angles on a circle and compared to distributions of interest [40], were used to investigate rhythmic periodicities in pup call response phases (Method S4). Following [21], we considered the values of the response phases as circular data falling between 0° and 360° . We obtained the circular mean (μ) (i.e., the average direction of the response phases calculated from the pup calls; Table S3). Then, we ran Rayleigh z-tests to investigate whether the distribution of response phases was uniform (e.g., arousal hypothesis) or showed a unimodal peak (Table S4) [21]. Subsequently, we tested for uniformity against a specified mean direction for the unimodal peak using a V-test [40–43].

Our data met the assumptions for circular statistics. We tested if the response phases in all four behavioural contexts followed a von Mises distribution using one-sample Watson tests (Table S5). With deviations from uniformity (null hypothesis von Mises distribution rejected), we used Kuiper's

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2 221 test, Watson's test, and Rao's spacing test, to confirm the p-value obtained from the Rayleigh test
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4 222 (Table S6) as suggested by Landler et al. [40]. More details are shown in Method S4.

5 223 We then tested whether response phase distributions varied depending on the presence of the
6
7 224 calling partner. We expected that vocally interacting pups would adjust their responses to broadcasted
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9 225 (1-way interaction) or real (2-way interaction) conspecific calls to avoid overlap and, hence, their
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11 226 response phases would show a unimodal distribution. Following previous work [21] and applying the
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13 227 V-test, we tested the null hypothesis of call response phase uniformity against two alternative
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15 228 unimodal departures: 0° (i.e., synchrony) and 90° (i.e., asynchrony). Using Watson's two-sample U^2
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17 229 test [44], we also compared the call phase distributions of 1) a pup calling alone vs. when responding
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19 230 to a broadcasted partner (pup I) and 2) a pup calling in the presence of a silent partner vs. when their
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21 231 partner was also calling (pups A-H). For interacting (1-way or 2-way) pups, we applied Watson's two-
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23 232 sample U^2 test to assess whether the type of partner (i.e., real or broadcasted) differentially affected
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25 233 the pups' response timing. We predicted that pups interacting with a real partner would show more
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27 234 adaptive call timing, thanks to potential communicative cues from other modalities. Lastly, we
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29 235 compared the distributions of call phases of the single pup vocalising alone to those of the paired pups
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31 236 when their partner was silent to test whether the simple presence of a silent partner affects individual
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33 237 call timing. In both behavioural contexts, we predicted that calling patterns for pups without a
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35 238 responsive partner would show a different rhythmic structure to those observed in interaction.

36 239 **Categorical rhythm** analysis tests whether the temporal intervals between signal onsets, as
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38 240 inferred from IOI ratios, are distributed categorically rather than uniformly. We predicted that
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40 241 empirical and simulated null ratio distributions (i.e., the expected distribution if no rhythmic
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42 242 categories exist) will not differ when a pup is alone or with a silent partner but will differ when a pup
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44 243 is vocally interacting. For vocally interacting pups, we predicted a significant peak in empirical ratio
45
46 244 distributions at the 4:1 small integer ratio based on the lone seal in [21], which called at approximately
47
48 245 one-quarter of the playback's period. All categorical rhythm analyses were done within bouts
49
50 246 following previous methodology (section Method S5) [23,24], with IOIs calculated in various ways
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52 247 depending on the behavioural context (Table S8, Figure 1). We used one-sample Kolmogorov-
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54 248 Smirnov (KS) tests to determine whether empirical IOI ratio distributions significantly differed from
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56 249 simulated null IOI ratio distributions. Our data met the one-sample KS test assumptions, namely that
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58 250 the sample is random and the theoretical distribution is continuous and fully defined. When the
59
60 251 empirical and simulated distributions were significantly different, we also looked for evidence of
61
62 252 small integer ratio (SIR) categorical rhythms—specifically at the 1:4, 1:3, 1:2, 1:1, 2:1, 3:1, and 4:1
63
64 253 ratios—which have been found in other species' vocalisations [23,24]. In these analyses, the empirical
65
66 254 ratio distributions were divided into “on-integer” and “off-integer” ratio bins (Table S7). On- and off-
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68 255 integer bin counts for each SIR were normalised by bin size and compared using a paired Wilcoxon

1
2 256 signed-rank test (a non-parametric test that allows for non-normality in the population data and
3
4 257 assumes paired differences are continuous, symmetrically distributed, and mutually independent).
5
6 258 When sample sizes allowed, we used two-sample KS tests (having met the assumption of mutual
7
8 259 independence of measurements within samples) to determine whether the ratio distributions of
9
10 260 individual pups differed across behavioural contexts.

11 261 The **Granger causality** test investigates whether the values of a time series A are better
12 262 predicted when considering the values from a second time series B, as opposed to only using values
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14 263 from time series A [45]. Here, we assessed whether the call timing of a pup partaking in a 1-way or
15
16 264 2-way vocal interaction can be predicted using the call timing of its partner. More specifically, to
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18 265 investigate whether the call timing of a pup differed in relation to the type of partner, we tested
19 266 whether there is a difference in predicting the time series of the pup interacting with a broadcasted
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21 267 partner vs. time series of the pups interacting with a real partner. Previous work showed that
22
23 268 individuals respond to conspecific calls with a non-random pattern [18–20,46]. We therefore expected
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25 269 that the time series of a pup can be better predicted considering the time series of a vocalising partner
26 270 rather than those of a broadcasted signal. In both the 1-way and 2-way interactive scenarios, we
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28 271 considered Granger causality at two levels: (1) the entire recording, regardless of the length of the
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30 272 pauses between consecutive calls, and (2) different bouts within each recorded session. We restricted
31 273 the analysis on the different bouts to call sequences that were long enough to generate accurate
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33 274 estimates (i.e., a minimum of five paired calls [47]). The bouts included in this analysis range from 5
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35 275 to 20 calls. We conducted the Granger causality test using call onsets and different *lag* measures, from
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37 276 one to five (Method S6), testing whether the previous one to five onsets in the first time series can be
38 277 used to better predict the second time series (Figures S5/S6, Table S11). For the 1-way interaction,
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40 278 we performed a one-way analysis, considering whether the pup's timing could be predicted using the
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42 279 playback timing. For the 2-way interaction, we performed a two-way analysis to assess whether the
43 280 two interacting pups influenced the timing of each other's calls.

45 281 We used **ADAM** to test for evidence of reactive error correction and predictive processes in the
46
47 282 1-way and 2-way interactive scenarios. ADAM consists of three computational modules that interact
48
49 283 via internal models of 'self' and 'other' that support one's own action planning and external event
50 284 prediction, respectively (Figure S2). The *adaptation module* compensates for synchronisation errors
51
52 285 by implementing error correction processes that alter the phase and/or period of an internal timekeeper
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54 286 controlling for action (here, call) timing. These error correction processes determine the provisional
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56 287 timing of the next planned action by providing input to an internal model of the 'self'. The
57 288 *anticipation module* computes the expected timing of upcoming events based on the weighted sum
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59 289 of two processes: the linear extrapolation of previous IOIs in the sequence and the copying (or
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290 'tracking') of the previous IOI, with the output informing temporal predictions generated by the

1
 2 291 ‘other’ internal model. Finally, a *joint module* integrates and compares the output of the adaptation
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 4 292 and anticipation modules and compensates for discrepancies by implementing an anticipatory error
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 6 293 correction process before the next motor command is issued. The joint module thus reduces potential
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 8 294 temporal mismatches between action plans in ‘self’ internal models and temporal predictions in
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 10 295 ‘other’ internal models, thereby regulating the balance between the integration (merging) and
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 12 296 segregation (distinction) of information about ‘self’ and ‘other’ [48,49]. Each process instantiated in
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 14 297 ADAM is controlled by an independent parameter, and the value of these parameters can be estimated
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 16 298 for a particular individual by fitting the model to behavioural time series data [26,27,50,51].
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 18 299 Parameter estimates were obtained for both the adaptation-only version of ADAM—which includes
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 20 300 phase correction and period correction—and the full (‘joint’) version—including period correction,
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 22 301 temporal prediction/tracking, and anticipatory error correction. Both versions of ADAM were applied
 23
 24 302 to each interactive context because it is not possible to know a priori whether the pups’ call sequences
 25
 26 303 (real or broadcasted) have a steady base tempo (for which adaptation is sufficient) or a systematically
 27
 28 304 changing tempo (which benefits from both anticipation and adaptation) (Method S7).
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 30 305

31
 32 306 **Table 1.** Summary table showing in order: research questions, analyses, contributing pups, predictions,
 33
 34 307 whether the data supports each prediction, statistical test(s) used, and result(s) obtained. The column
 35
 36 308 “Supported by data?” has three possible answers: results support the prediction (Y), results only partially
 37
 38 309 support the prediction (Partial), and results do not support the prediction (N). Due to sample size and/or
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 40 310 analytical requirements, not all pup data could be used in each analysis. The acoustic variables of interest for
 41
 42 311 the different analytical approaches were: response phases (circular statistics), IOI ratios (categorical rhythms),
 43
 44 312 IOIs (Granger causality, ADAM), and asynchronies (ADAM).
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 46 313

Research question	Analytical approaches	Pups	Prediction	Supported by data?	Statistical test(s) and result(s)
<i>Temporal domain, Q1:</i> Does the presence of a calling partner affect the call timing of individual pups?	Circular statistics	A-I	Pups will not vocalise at random points in time.	Y	Rayleigh test: Unimodal distribution of response phases.
			Pups will call in asynchrony to avoid overlap during vocal interactions.	Y	V-test: Pup calls start at one-quarter of the partner’s period
			Response phases will be affected by the presence of a vocalising partner.	Y	Watson’s U^2 test: Response phase distributions differ between non-interactive and interactive contexts.

	Categorical rhythms	A, B, C, E, H, I	Empirical and chance ratio distributions will only significantly differ when pups are vocally interacting.	Partial	1-sample KS tests: Simulated and empirical ratio distributions are rarely significantly different (exceptions: pup I alone, pup I 1-way, pup B 2-way).
		A, B, I	Vocally interacting pups will have a significant peak at the 4:1 SIR.	N	Paired Wilcoxon signed-rank test: No significant peaks at any of the tested small integer ratios.
			Ratio distributions of individual pups will differ across behavioural contexts.	Y	2-sample KS tests: Ratio distributions significantly differed for the same individuals in different behavioural contexts.
Social domain, Q2: Does the type of calling partner (real or broadcasted) affect the call timing of individual pups?	Circular statistics	A-I	Pups interacting with a real partner will show more adaptive call timing than the pup interacting with a broadcasted partner.	N	Watson's U^2 test: No difference in response phases between 1-way and 2-way interactions.
	Granger causality	A, B, C, D, E, F, I	The time series of a pup will be better predicted considering the time series of a vocalising partner rather than the time series of a broadcasted signal.	Y	Bidirectional & unidirectional causality: Interaction with a real partner impacted the pup's vocal behaviour more than the playback. Mutual temporal adaptation among pairs of vocally interacting pups.
Social domain, Q3: When the focal pup is vocalising, does the presence of a silent partner (vs. no partner) affect call timing?	Circular statistics	A-I	The calling pattern of pups will show similar rhythmic structure in both the alone and silent partner conditions, as no vocal interaction is taking place in both cases.	Y	Watson's U^2 test: No difference between response phase distributions of pup calling alone and pups calling with a silent partner.

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Cognitive domain, Q4: <i>Which timing mechanisms are used by pups during vocal interactions?</i>	ADAM	A, B, I	In the 1-way interaction, pups may show sensitivity to (non-)interactivity which would be reflected by parameter changes over repeated sessions. The 2-way interaction may be mediated by basic temporal adaptation and possibly higher-level anticipatory timing.	Partial	1-way interaction: Temporal anticipation, and to a lesser extent also adaptation, decreased across the playback sessions, and was absent in the final session. 2-way interaction: Clear evidence for temporal adaptation, with differing parameter estimates for each seal pup suggesting the emergence of different interactive roles.
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3. Results

3.1. Does the presence of a calling partner affect the call timing of individual pups? (Q1)

All pups' data entered the circular statistics analysis. Running the Rayleigh test, we found that the response phase distribution was uniform for pup I which was recorded alone ($z = 0.04$, $p = 0.254$; Figure 2A), whereas it was non-uniform for pups A-H which were recorded with a silent partner ($z = 0.11$, $p < 0.001$; Figure 2A; Table 1). This non-uniformity may have been driven by the individual contributions of pups B and C, which had non-uniformly distributed response phases (Table S4), whereas the other six pups had a uniform distribution. The Rayleigh tests run anew in the interactive contexts, showed that the response phase distributions of pup calls were unimodal in both the 1-way (pup I: $z = 0.39$, $p < 0.001$) and 2-way (pups A - H: $z = 0.41$, $p < 0.001$) interactions (Figure 2B; Table 1). Applying the V-test in both contexts, the direction of the response phases did not statistically match 0° (1-way: $z = -0.02$, $p = 0.587$; 2-way: $z = 0.06$, $p = 0.110$), suggesting that pups did not synchronise with their partner (real or broadcasted). However, the response phase direction did match 90° (1-way: $z = 0.38$, 2-way: $z = 0.41$, $p < 0.001$), supporting the previously reported evidence of asynchronous calling behaviour [21]. A Watson's two-sample U^2 test confirmed that the response phase distributions significantly differed between the alone vs. 1-way interaction context for pup I ($U^2 = 1.76$, $p < 0.001$), and between the silent partner vs. 2-way interaction context for pups A-H ($U^2 = 0.78$, $p < 0.001$, Figure S3; Table 1). Finally, the circular standard deviation values were higher for the alone and silent partner contexts compared to both interactive vocal contexts, indicating a larger dispersion of the response phases for the former conditions. This outcome is also confirmed by the values for the mean resultant length.

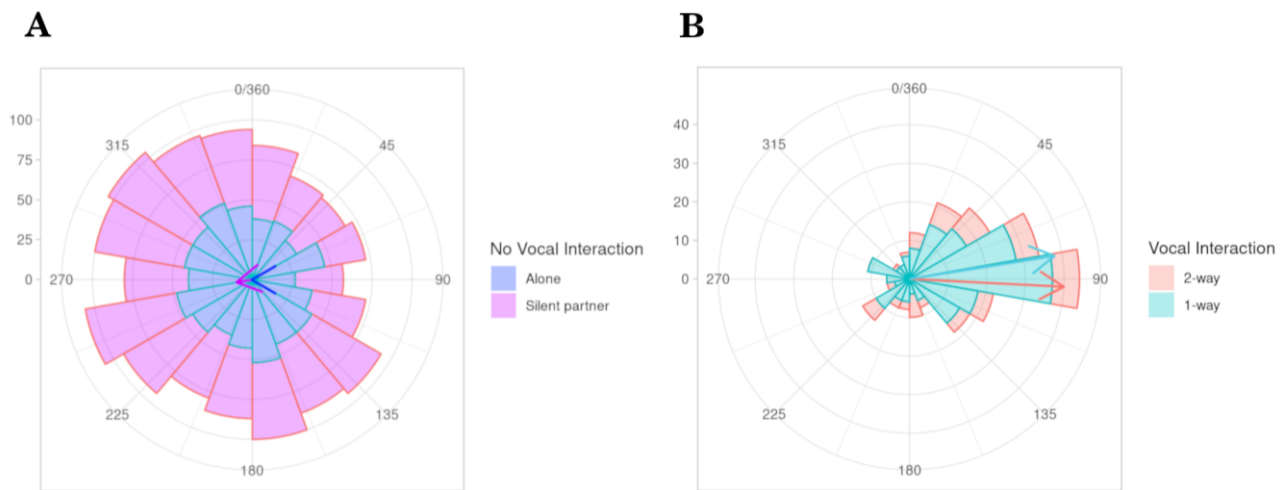


Figure 2. Circular histogram plots (bin width = 20°) showing response phases in (A) both types of behavioural contexts with no vocal interaction (alone/silent partner), and (B) in both types of vocal interaction contexts (1-way/2-way). Angles are measured in degrees starting from 0° and going clockwise to 360°. The arrows indicate the circular mean (μ) and colours correspond to the different behavioural contexts. The length of the arrow corresponds to the value of the mean resultant length (ρ).

In the categorical rhythm analyses, the empirical ratio distribution was significantly different from chance when pup I was recorded alone (Figure 3A) and during the 1-way interaction (Figure 3C). In both contexts, there was no evidence of significant peaks at any of the tested ratios (Table 1). When the playback calls were disregarded from IOI calculations (Figure 3B), there was no significant difference in empirical and simulated ratio distributions for pup I. However, pairwise KS tests showed that the ratio distributions significantly differed when comparing each of the three behavioural contexts (alone vs. 1-way interaction disregarding playback vs. 1-way interaction when pup I responds) to each other (Table S10; Table 1). For the five pups that were well-sampled in the silent partner context (pups A, B, C, E, and H; Table S8), the empirical ratio distributions did not significantly differ from chance (Table S9, Figures 3/S4, Method S4). Finally, when considering 2-way interactions, only pups A and B were well-sampled enough (i.e., had at least ten ratios for both the silent partner and 2-way interaction contexts) to compare, but the empirical and simulated ratio distributions were significantly different only when pup B was the responder (Figure 3; Table S8; Table S9). Once again, there were no significant peaks at any of the tested ratios for pup B. For both pups A and B, the empirical ratio distributions significantly differed when comparing different behavioural contexts (Table S10). Collectively, there was thus little evidence of SIR rhythmic categories in pup calls, but IOI ratios did significantly differ when looking at the same individuals in different behavioural contexts (Table 1).

Thus, the results from both analyses suggest that the *presence* of a calling partner does affect the call timing of the focal pup, in terms of both call response phases and IOI ratios.

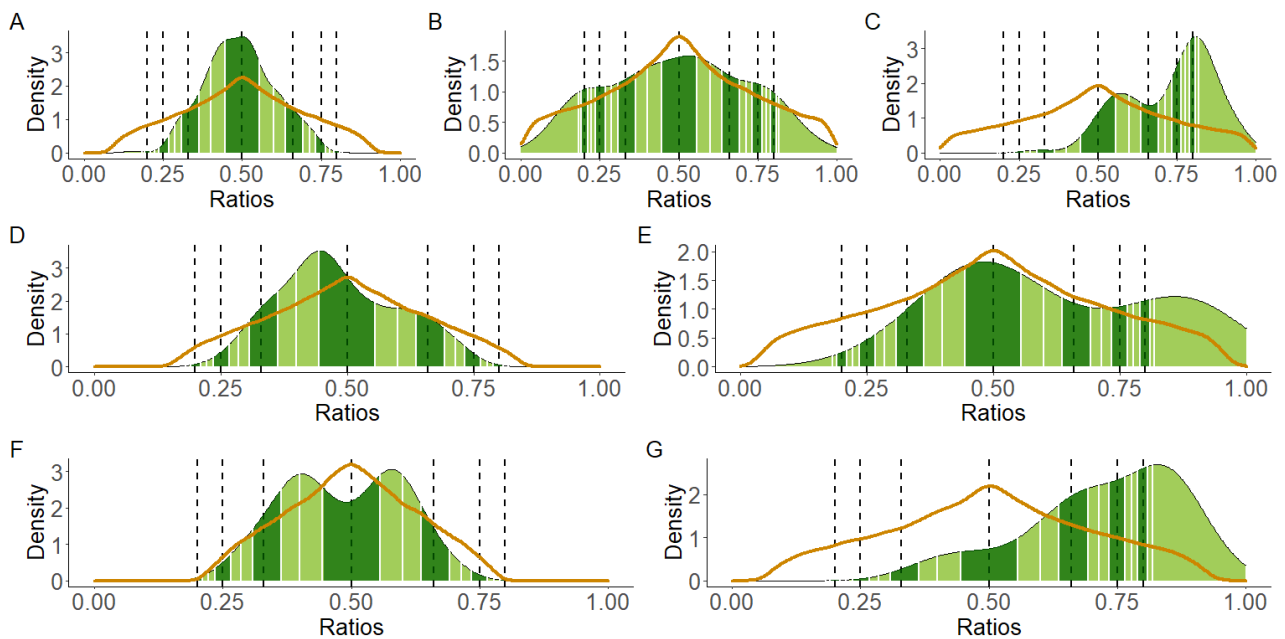


Figure 3. IOI ratio density plots for pups in different behavioural contexts. Pup I: (A) alone, (B) 1-way interaction (disregarding playback), (C) 1-way interaction (responding to playback). Pup A: (D) silent partner, (E) 2-way interaction (responding to partner). Pup B: (F) silent partner, (G) 2-way interaction (responding to partner). For each plot, the dashed vertical lines indicate, from left to right, 1:4, 1:3, 1:2, 1:1 (i.e., isochrony), 2:1, 3:1, and 4:1 small integer ratios. On-integer ratio ranges are in dark green and off-integer ratio ranges are in light green, with white lines and black dashed lines denoting bin boundaries. The orange curves indicate the ratio distribution expected under a uniform distribution if no rhythm categories exist. The empirical ratio distribution significantly differed from the simulated ratio distribution for panels (A), (C), and (G) only. Note that the scale of the y-axes differ.

3.2. Does the type of calling partner (real or broadcasted) affect the call timing of individual pups? (Q2)

To address this research question, we once again used circular statistics and the response phase distributions of all nine pups. Specifically, we compared calls from pup I during the playback (1-way interaction) with calls of pups A-H when their partner was also calling (2-way interaction). A Watson's two-sample U^2 test statistically confirmed that the response phase distributions did not differ between the 1-way and 2-way vocal interactions ($U^2 = 0.07$, $p > 0.10$; Table 1).

Interestingly, however, the Granger causality results from seven pups (A, B, C, D, E, F, I) showed that call timing behaviour differed depending on the type of partner (Table 1). For the 1-way interaction, five different playback sessions featuring pup I were considered (ranging from 34 to 121 paired calls) and the timing of the pup's calls were never significantly predicted by the timing of the playback (Table S11, Figure S5). For the 2-way interaction, five different recording sessions were considered (ranging from 8 to 71 paired onsets). We found that in two sessions, the timing of the first pup did not significantly predict the timing of the second, in either direction (pair A>B and B>A; pair E>F and F>E; Table S11, Figure S6B/S6D). However, in two other sessions, the timing of a pup was significantly predicted by the calling partner in both directions, across different lag values (A>B: lag-

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2 391 1, lag-3, lag-4, lag-5; B>A: lag-3, lag-4, lag-5; C>D and D>C: lag-2 and lag-3; Table S11, Figure
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4 392 S6B/S6C). In the last session, the timing of pup A could be predicted by that of pup B, while we found
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6 393 no indication of temporal adjustment for pup B. At the bout level, we restricted our analyses to four
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8 394 series of paired onsets featuring pups A and B (as they were the only pup pair that met the sample
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10 395 size requirements). In this last scenario, only the timing of pup B was significantly influenced by pup
11 396 A (Figure S6A).

12 397 While the circular statistics results thus suggest that the type of calling partner (real vs.
13
14 398 broadcasted) does not affect focal pup call timing, the Granger causality results suggest that in certain
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16 399 2-way (but not 1-way) interactions, focal pup call timing can be predicted by the partner's call timing.
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19 401 **3.3. When the focal pup is vocalising, does the presence of a silent partner (vs. no partner)** 20 21 402 **affect call timing? (Q3)**

22
23 403 Using circular statistics, we compared the calls of pup I recorded alone with those of the 8 other
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25 404 pups (A-H) recorded with a silent partner present. Watson's two-sample U^2 test results show that the
26 405 response phase distributions did not statistically differ between the two contexts ($U^2 = 0.10, p > 0.05$).
27
28 406 In other words, having a silent partner was essentially the same as having no partner—in terms of the
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30 407 effect on focal pup response phase distributions—for the pups in our study. This is intuitive, given
31 408 that in both behavioural contexts, there is no acoustic stimuli to “respond” to.
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34 35 410 **3.4. Which timing mechanisms are used by pups during vocal interactions? (Q4)**

36 411 ADAM parameter estimation was conducted on call data from all five playback sessions
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38 412 featuring pup I (1-way, Figure 4 A/B), but was restricted to pups A and B for the 2-way interactions
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40 413 due to sample size limitations (Figure 4 C/D). Interactive vocal bouts were concatenated to obtain a
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42 414 time series length which would provide reliable ADAM parameter estimates. A simulation test then
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44 415 ensured that the estimates were not compromised by differing sequence lengths or by the
45 416 concatenation procedure (Method S7). The reliability of observed parameter estimates was tested by
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47 417 comparison against corresponding values for randomly permuted data (Method S7). The quality of
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49 418 the fits to the data did not differ significantly between versions of ADAM (Method S7). Results for
50 419 the 1-way interaction featuring pup I were remarkable with regards to typical human data (e.g.
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52 420 [26,27]) as most significant parameters were negative in sign (Figure 4A/B, Tables S13/S14).
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54 421 Negative phase and period correction estimates indicate that calling earlier will lead to a shortening
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56 422 of the next IOI, while calling later will lead to a lengthening of the next IOI. Negative
57 423 prediction/tracking estimates mean that when the playback's IOIs increase (i.e., deceleration), the
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59 424 pup's IOIs will decrease (i.e., acceleration), and vice versa. This systematically enhances the timing
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425 distinction between calls, possibly testing the responsiveness of the partner (i.e., playback) by

introducing timing asynchronies and gauging their effects. It is worth noting that evidence of such behaviour generally decreased across the five playback sessions, with no significant parameter estimates emerging in the final session.

For the 2-way interaction (Figure 4C/D, Tables S13/S14), the parameter estimation procedure was run twice, each time with one of the two pups serving as the focal individual and the other as the external reference. With this procedure, similar parameter estimates for each pup would indicate a symmetrical pattern of influence, whereas different estimates would indicate asymmetrical influence. Results for this type of vocal interaction showed evidence for temporal adaptation. In particular, parameter estimates were consistent with pup A engaging in period correction while pup B engaged in both phase and period correction. Period correction estimates were positive in sign for pup A and negative for pup B. Pup A's positive period correction estimates suggest that calling earlier will lead to a lengthening of the next IOI, whereas calling later will lead to a shortening of the next interval. Pup B exhibited the opposite effect but to a lesser degree. Pup A thus implemented a timing mechanism that increased the similarity in their calling rates, while pup B implemented a timing mechanism that increased the distinction in calling rates. It should be noted, however, that the observed parameter estimates do not necessarily reflect individual call styles per se, but rather the roles that dynamically emerge within the context of this specific pairing of pups.

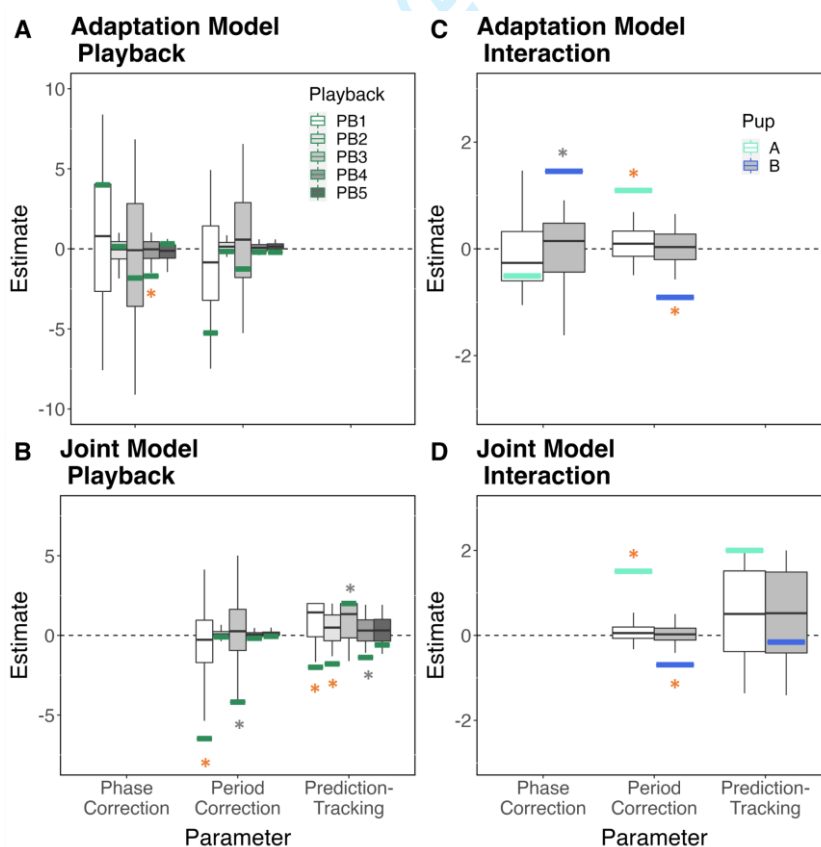


Figure 4. ADAM parameter estimates for seal pups A, B, and I. Left panels (A & B) show parameter estimates for pup I in five playback sessions (1-way interaction); right panels (C & D) show estimates for pups A and B (2-way interaction). Top panels (A & C) show phase correction and period estimates obtained with the adaptation-only version of ADAM; bottom panels (B & D) show period correction and prediction-tracking estimates for the full 'joint' model (anticipatory error correction estimates are not shown). Parameter estimates are shown separately for pup A relative to pup B (aquamarine bars) and pup B relative to pup A (blue bars) in the recording session, and for pup I (green bars) relative to playback calls in separate playback sessions (PB1-PB5). Corresponding parameter estimates for randomly permuted data from each session are represented by box plots, with the central horizontal line indicating the median, the bottom and top edges of the box indicating the 25th and 75th percentiles, and the whiskers indicating the 5th and 95th percentiles. Real estimates with asterisks are significantly different from permuted data estimates at the 2-tailed (orange) or 1-tailed (grey) level.

4. Discussion

This study sought to provide a methodological proof of concept for quantifying vocal rhythmicity in non-human animal interactive communication. Particularly, we showed how complementary methodologies can be used to test whether the (Q1) presence and (Q2) type of a vocalising partner, or the (Q3) presence of a silent partner affect patterns in animal communication (Table 1). We also investigated which (Q4) underlying cognitive mechanisms potentially play a role in vocal interactions (Table 1). The different analytical techniques proved fruitful; combining and contrasting their results could highlight nuances in rhythmic behaviour. Nonetheless, our sample size is undeniably small, and our opportunistic design (e.g., mixing within- and between-individual comparisons) cannot provide strong inference. We believe that our experimental setup, combined with the approaches we present, can be adapted and expanded in future work to better understand the temporal, social, and cognitive processes underlying interactive communication in animals.

Q1. The presence of a vocalising partner influences rhythm in vocal interactions

The prediction of overlap avoidance was supported by circular statistics, which showed that the distributions of response phase angles were unimodal. When vocally interacting, pups responded at approximately one-quarter of the playback/real partner calling period (90°) and showed phase angles significantly different from 0° , supporting previous results from one individual (pup I) [21]. Pups responding to conspecifics seem to time their calls to avoid overlap, consistently de-synchronizing their call onsets. When pups were recorded alone or with a silent partner, the distribution of phase angles was uniform, with no significant rhythmic pattern. Our findings confirm and extend previous outcomes [21]; in our limited sample, pups not only react to playbacks with asynchrony, but also respond to conspecific partner calls in an asynchronous manner.

Regarding categorical rhythms, the empirical ratio distribution did not significantly differ from the distribution expected by chance if IOIs were uniformly distributed for most pup/behavioural context combinations (7/10). For the remaining three combinations (pup I alone; pup I, 1-way interaction; pup B, 2-way interaction), there was no significant evidence that call timing exhibited

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2 486 categorical rhythms at the seven tested small integer ratios. This includes the 4:1 ratio, which we
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4 487 hypothesised would frequently occur when pups were vocally interacting with playback stimuli or
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6 488 partners based on previous work [21]. Importantly, however, the empirical ratio distributions
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8 489 significantly differed across behavioural context conditions for the three pups (A, B, I) for whom such
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10 490 comparisons were possible. When alone or with a silent partner, pup calls generally showed unimodal
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12 491 ratio distributions centred around isochrony, whereas calls emitted by vocally interacting pups
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14 492 showed a clear right-shifted peak, or a second peak to the right of isochrony, indicating that the pup's
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16 493 IOIs during vocal interactions were generally shorter than the playback's/partner's IOIs. This context-
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18 494 dependent asymmetry bolsters results related to Q4, namely that the presence of vocalising partner
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20 495 can significantly impact pup vocal behaviour, with interacting individuals trying to prevent call
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22 496 overlap. Roeske and colleagues [23] hypothesised that categorical rhythms may be prevalent in calls
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24 497 meant to attract and hold conspecific attention, such as the calls pups use to attract the attention of
25
26 498 their mothers. We did not find evidence of rhythm categories at seven tested ratios; this negative result
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28 499 has methodological value, highlighting that not all species that produce attention-seeking
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30 500 vocalisations show integer ratio categories.

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32 501 A vocal interaction with non-adaptive playback stimuli (1-way) may represent a limitation to
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34 502 studying spontaneous vocal production. The extent of this limitation can be gauged by comparing
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36 503 results to data from vocal interactions with a real partner (2-way), and with the use of complementary
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38 504 analytical methodologies, such as categorical rhythm analysis and circular statistics.

39 505 **Q2. Type of calling partner (real or broadcasted) partly affects rhythm in interaction.**

40 506 Findings from Q2 show contrasting results. Call phases were statistically the same no matter if
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42 507 pups could interactively adjust their call timing to each other (2-way) or not (in 1-way). Partly in
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44 508 contrast with this, the Granger causality analysis showed how vocally interacting with a real
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46 509 individual impacted the pup's vocal behaviour more than interacting with a broadcasted partner
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48 510 Indeed, we found evidence of mutual temporal adaptation among pairs of vocally interacting pups
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50 511 and, consistent with a recent hypothesis [6], conspecific interactions can be facilitated by the
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52 512 reciprocal adjustment of timing behaviour. In contrast, we found little evidence that a pup adjusts the
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54 513 time series of its calls to a playback series. Indeed, in most cases, the pup's call timing could not be
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56 514 predicted by the playback's call timing.

57 515 Together, findings from circular statistics (Q1) and Granger causality (Q2) point towards a
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59 516 directionality-overlap avoidance relationship, which has also been suggested for other non-human
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61 517 species (e.g., primates [18,52]; birds [53]; amphibians [54]; seals [55]). Interestingly, when infant
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63 518 marmosets interact with their parents, the probability that their vocalisations will overlap with those
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2 520 of adults decreases over time [22], suggesting that turn-taking in some mammals is a learned vocal
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4 521 behaviour scaffolded by active parental feedback [39].

7 523 **Q3. A silent partner does not trigger call rhythmicity**

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9 524 Circular statistics indicated that pups did not show any periodic pattern both, either when calling
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11 525 alone or with a silent partner present (Q1). This is consistent with the fact that wild pups produce calls
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13 526 to attract a silent mother [36]: if no other calling conspecifics are present, there is no need to adjust
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15 527 one's call timing and vocalisations are produced with a random onset. Moreover, given that the
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17 528 response phase distributions did not differ between pups recorded with a silent partner or alone, it
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19 529 suggests that the presence of a silent partner did not trigger variable calling behaviour in our study
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21 530 population.

22 23 532 **Q4. Purported timing mechanisms for vocal interactions**

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25 533 The ADAM analysis suggests that seal pups may perceive temporal patterns [56], which arise
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27 534 between their calls and those of others, and react to them by adopting different mechanisms for
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29 535 temporal adaptation. The negative parameter estimates that we observed in the 1-way interaction
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31 536 sessions (consistent with enhancing the distinction between calls) could reflect attempts to lead the
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33 537 temporal interaction or even to test the responsiveness of the (broadcasted) partner by introducing
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35 538 timing perturbations and gauging their effects. The decrease of temporal adaptation and/or
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37 539 anticipation observed across playback sessions is consistent with a gradual process of habituation,
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39 540 with the pup possibly learning that the playback is non-interactive. Harbour seals are capable of
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41 541 acoustic recognition based on habituation paradigms; they can discriminate among different stimuli
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43 542 and selectively habituate to them [57]. The lack of temporal adaptation to the playback stimulus we
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45 543 observed in a seal pup may entail similar habituation processes. From a comparative perspective,
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47 544 these findings also suggest a sensitivity to social contingency that may be analogous to capacities in
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49 545 human infants, who become disinterested and display fewer signs of positive affect during vocal
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51 546 interactions with non-responsive or delayed video recordings of their mothers [58–62]. Future studies
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53 547 could address the role of temporal contingency by using interactive playback sequences [63–65].

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55 548 Ours constitutes the first attempt to apply ADAM to non-human animals. On the technical side,
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57 549 this necessitated the validation of an approach where brief interactive vocal bouts were concatenated
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59 550 to produce longer time series and thereby reduce the risk of model overfitting (Discussion S1).
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61 551 Demonstrating the utility of this procedure opens the door to applying the model in a wider range of
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63 552 behavioural contexts. Nevertheless, caveats are necessary when interpreting the seal data in light of
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65 553 previous work with ADAM in humans, where individuals intentionally produce movements, whose
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67 554 sensory effects occur simultaneously with rhythmically regular sounds (e.g. [26,27]). Assumptions

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2 555 about intentionality and simultaneity may not apply to seal pup vocal interactions or rhythmic
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4 556 interactions in other animals [6,9]. Points of convergence in the main outcomes of the complementary
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6 557 analysis techniques suggest that ADAM, like categorical rhythm analysis, circular statistics, and
7 558 Granger causality, may also be robust and informative under such conditions.
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9 559 10 11 560 **5. Conclusions**

12 561 Crucially, our work highlights the efficacy of combining multiple methods to study rhythmic
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14 562 vocal behaviour. Our approaches vary in the degree to which they capture global temporal
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16 563 characteristics across events vs. local temporal dependencies between events. Global measures (e.g.,
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18 564 from circular statistics or categorical rhythm analysis) reveal predominant rhythmic features of a
19 565 vocal interaction while local time series measures (e.g., from Granger causality or ADAM) provide
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21 566 information about how these features might arise. Through this approach we could tease apart rhythm
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23 567 nuances in our dataset, further develop harbour seals as a model species, and demonstrate how certain
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25 568 analyses often restricted to humans, such as categorical rhythms (but see [23,24]) and ADAM, can be
26 569 applied to non-human animals. The categorical rhythm and circular statistical analyses tackled similar
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28 570 questions from different angles, namely whether the distributions of IOI ratios (the former) or call
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30 571 response phases (the latter) significantly differed across behavioural contexts. The categorical rhythm
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32 572 analyses also sought to determine whether the rhythmicity of pup calling behaviour conforms to small
33 573 integer ratios. Our negative result is, to our knowledge, the first published case of a species for which
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35 574 categorical rhythms are clearly absent from vocalisations, which adds to understanding of how, why,
36
37 575 and when such rhythms evolve in communication systems. Time series analyses such as Granger
38 576 causality allowed testing for timing adjustment. In the case of ADAM, mechanisms of temporal
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40 577 adaptation and anticipation that have previously been used to describe rhythmic behaviour in humans
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42 578 [66] were used to describe rhythmic behaviour in seals. Interestingly, the ADAM model provides an
43 579 empirical warning about potential seal pup habituation effects when vocally interacting with a
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45 580 recorded partner.
46

47 581 Though our sample size is small, studies on single individuals are not unusual in comparative
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49 582 research [20,67]. Nevertheless, it is possible that the lack of adjustment to a playback, the adaptation
50 583 to a real individual, or both, reflect a peculiar vocal behaviour of the individuals we tested and cannot
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52 584 be generalised to the species as a whole. The pups in this study were in a temporarily captive setting,
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54 585 albeit in acoustic proximity to other individuals, similar to conditions they would experience in
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56 586 nature. Unfortunately, vocal development in harbour seal pups has not been studied in wild colonies,
57 587 hence we do not know whether captivity affects their vocal development. We do know, however, that
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59 588 pups vocally interact with neighbouring pups in the colony and not with their silent mothers; hence
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1
2 589 the turn-taking behaviour observed in our captive conditions might extend to the same behaviour in
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4 590 wild conspecifics.

5 591 Motivation for an individual to respond and engage in an interaction, with the closest partner in
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7 592 the colony, may depend on the degree of participation signalled by the partner. This, in turn, may be
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9 593 triggered by individual-specific behaviours or by cues from other modalities. Multimodal
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11 594 communication should be the target of future studies since we cannot assume that such interactions
12 595 are limited to acoustic cues. Despite these limitations, our study shows that adopting multiple
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14 596 complementary approaches can be a fruitful way to study rhythmic interactivity in non-human animal
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16 597 communication.

17 598

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20
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22
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24
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26 603 the rehabilitation process of the seal pups. We are thankful to Chiara De Gregorio for sharing the R
27
28 604 code used for the categorical rhythm analyses and to Laura Verga for providing helpful comments on
29
30 605 a draft of this manuscript.

1

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3

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Measuring rhythms of vocal interactions: A proof of principle in harbour seal pups

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Abstract

Rhythmic patterns in interactive contexts characterise human behaviours such as conversational turn-taking. These timed patterns are also present in other animals, and often described as rhythm. Understanding fine-grained temporal adjustments in interaction requires complementary quantitative methodologies. Here, we showcase how vocal interactive rhythmicity in a non-human animal can be quantified using a multi-method approach. We record vocal interactions in harbour seal pups (*Phoca vitulina*) under controlled conditions. We analyse these data by combining analytical approaches, namely categorical rhythm analysis, circular statistics, and time series analyses. We test whether pups' vocal rhythmicity varies across behavioural contexts depending on the absence or presence of a calling partner. Four research questions illustrate which analytical approaches are complementary vs. orthogonal. For our data, circular statistics and categorical rhythms suggest that a calling partner affects a pup's call timing. Granger causality suggests that pups predictively adjust their call timing when interacting with a real partner. Lastly, the ADaptation and Anticipation Model (ADAM) estimates statistical parameters for a potential mechanism of temporal adaptation and anticipation. Our analytical complementary approach constitutes a proof of concept; it shows feasibility in applying typically unrelated techniques to seals to quantify vocal rhythmic interactivity across behavioural contexts.

Keywords: Behavioural interaction, asynchrony, circular statistics, categorical rhythms, time series analysis, interactive vocal rhythm

1. Introduction & methodological approaches

1.1. Rhythmic interaction and turn-taking

Humans adopt precise signalling behaviours to exchange information [1,2]. **No matter the signal modality (e.g., acoustic, visual), an interactive event between sender and receiver is governed by a timed structure [3–6].** The structured exchange of communicative turns (i.e., turn taking) characterises our capacity for social interaction, enabling us to communicate with others [7,8]. The study of interactive rhythms—how two (or more) individuals coordinate their signalling in time—is an emerging field of research, with more recent work extending structural analyses of communication signals, once restricted to human spoken conversation, to other species [3,9]. Turn-taking in communication has been documented in primates [10] and in other non-primate species [6,11–13]. **For example, call exchanges in adult common marmoset monkeys (*Callithrix jacchus*) exhibit coupled oscillator dynamics, like those observed in human turn-taking [14].** Two key components of turn-taking are the flexible organisation and distribution of turns, and the temporal relationship between adjacent turns [11]. In humans, face-to-face interactions require participants to be, among others, both socially and temporally sensitive [15]. Does behavioural context also affect signal timing in non-human animals? Comparative investigations on interactive vocal timing in mammals may help uncover shared turn-taking mechanisms, potentially providing more insights into their evolution.

1.2. Methodological approaches and challenges for studying rhythmic interaction

Expanding the human turn-taking framework to other species is currently hindered by, among other things, lack of suitable methodological approaches [11,16]. Cross-species frameworks exist [17], but open questions still remain in animal face-to-face interaction, such as: Which analytical methodologies used to investigate turn-taking in humans may reveal temporal adjustments in other species? Can turn-taking arise from non-cooperative behavioural interactions? Can methods developed for individual rhythm analyses be used to study rhythmic interaction? Can parametric models for human rhythmic prediction and reaction detect similar features in other species? These open questions require suitable animal models and quantitative methods.

Different forms of vocal rhythmic interaction, such as synchronous chorusing and turn-taking, have been mainly studied in mammals within a cooperative dynamic, like parent-infant and male-female dyads. Time series analyses like Granger causality have shown temporal interdependence between vocalisations in male-female pairs [18,19] and movements [20] of non-human primates. Circular statistics is another method to study timing adjustments in interactions, and has been used in previous animal work, including a seal pup playback experiment [21] and a study on parent-infant monkey interaction [22]. Categorical rhythms—those for which the temporal intervals between signal onsets are distributed categorically rather than uniformly—are a universal characteristic of human

1
2 90 music, which is often produced in an interactive context [23]. Similar rhythms are also present in non-
3
4 91 human animal songs (e.g., thrush nightingales [23], indris [24], but whether such rhythms characterise
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6 92 other interactive non-song vocalisations, such as animal calls, is unknown [23,24]. Roeske and
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8 93 colleagues [23] hypothesised that categorical rhythms play a role in calls produced to attract and hold
9
10 94 conspecific attention, by making sequences of vocalisations more predictable to listeners. Categorical
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12 95 rhythm analyses could therefore be an interesting method to test the predictability of vocal sequences
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14 96 in non-human animal interactions. Lastly, the ADaptation and Anticipation Model (ADAM),
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16 97 originally developed to model the mechanisms for interpersonal coordination in humans [25], has
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18 98 been adopted to probe sensorimotor and cognitive mechanisms underlying temporal dynamics in
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20 99 interaction [26,27]. Although ADAM is designed for ‘simultaneous chorusing’, it could also be used
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22 100 for a mixture of bouts of synchrony, turn-taking, and other regimes [21,28].

21 101 In this proof of concept study, we showcase how these methodological tools— Granger
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23 102 causality, circular statistics, categorical rhythm analysis, and ADAM—can be applied to a new animal
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25 103 model: the harbour seal (*Phoca vitulina*). To illustrate the utility and compatibility of these different
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27 104 analytical methods, we show how they can be used to better understand the rhythmic communication
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29 105 of a small sample of harbour seal pups in different behavioural contexts.

31 107 1.3. Our animal model

32
33 108 The “vocal learning-beat perception and synchronisation” (VL-BPS) hypothesis states that only
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35 109 vocal learning species—those capable of producing new vocalisations or modifying existing ones
36
37 110 based on auditory experience—may possess advanced rhythmic abilities [29,30]. This hypothesis is
38
39 111 inherently cross-modal: it suggests a strong link between audition and timed movement. For example,
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41 112 Snowball, a sulphur-crested cockatoo (*Cacatua galerita eleonora*), was shown to perceive auditory
42
43 113 rhythms at different tempi and to predictively synchronise his body movements to them [31]. Parrots
44
45 114 are phylogenetically distant from humans and, among mammals, pinnipeds (seals, sea lions, and
46
47 115 walruses) are one of the vocal learning groups (besides humans, bats, elephants, and cetaceans).
48
49 116 Pinnipeds may well be the best mammalian model for testing the VL-BPS hypothesis—the ability to
50
51 117 extract a beat from periodic acoustic stimuli and entrain to it in a predictive and adaptive manner—
52
53 118 since some species showed vocal mimicry and plasticity [32,33] and others can keep a beat [34].
54
55 119 These characteristics, paralleling human abilities, make pinnipeds an ideal animal clade for
56
57 120 comparative research on the origins of rhythmic communicative behaviour.

55 121 Harbour seals exhibit both vocal flexibility [33,35] and rhythmic interactivity [21], and are
56
57 122 particularly vocal in the first few weeks of life [36]. During the lactation period, harbour seal pups
58
59 123 emit ‘mother attraction calls’ (hereafter ‘calls’) to draw their mothers’ attention [37]. Mothers are
60
124 silent and use the individual vocal signatures in these calls to recognize their pups [36,38]. Against

1
2 125 the acoustically complex backdrop of large mother-pup rookeries, rhythmically tuned pup calls could
3
4 126 constitute a socio-ecologically selected trait that allows individual pups to avoid conspecific call
5
6 127 overlap by adjusting the timing of their own call onsets. Such timing plasticity could allow a pup to
7
8 128 be more acoustically conspicuous and increase its chances of successful reunions with its mother.
9 129 Unlike cooperative types of turn-taking (e.g., in humans and in common marmosets (*Callithrix*
10
11 130 *jacchus*) [39]) harbour seal pups' interactions are a by-product of neighbouring pups vocalising to
12
13 131 attract their silent mothers, and are thus probably competitive.

14 132 To date, only two papers studied vocal rhythms in harbour seals, crucially both focusing on
15
16 133 single individuals [21,28]. The first study was a playback experiment in which a pup vocally
17
18 134 interacted with sounds broadcasted from a loudspeaker [21]. The pup adjusted the timing of its calls
19
20 135 in an asynchronous manner by responding to the broadcasted conspecific calls with a non-uniformly
21
22 136 distributed response phase whose mean approximated 90° [21]. The second study looked at the
23
24 137 presence and development of vocal rhythms in three harbour seal pups [28]. Complementary
25
26 138 analytical approaches showed how the pups' *individual* calling patterns gained more rhythmic
27
28 139 structure over time [28]. However, a major limitation of both studies was the lack of sociality (i.e.,
29
30 140 individuals were tested alone) and, by extension, interactivity (i.e., the stimuli did not adapt to the
31
32 141 response of the tested animals).

33 143 1.4. Aims & research questions

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35 144 In this work, we show how vocal interactive rhythmicity in non-human animals can be
36
37 145 quantified using a multi-method approach spanning various research domains (e.g., temporal, social,
38
39 146 cognitive) (Table 1). We illustrate this approach through four research questions, all of which relate
40
41 147 back to whether harbour seal vocal interactive rhythmicity varies in different behavioural contexts
42
43 148 (Table 1). While our sample sizes are too small to enable species-wide inferences, they are sufficient
44
45 149 to illustrate how methods typically used to study human communication can be adopted to study
46
47 150 interactivity in animal communication. The goal of this paper is thus to outline a quantitative roadmap
48
49 151 that future research can follow. Circular statistics and categorical rhythm analysis are used to address
50
51 152 the first question about temporal adjustment in interaction: “*does the presence of a calling partner*
52
53 153 *affect the call timing of individual pups?*” (Q1). The next two questions consider the effect of
54
55 154 behavioural context on temporal adjustment: “*does the type of calling partner (real or broadcasted)*
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57 155 *affect the call timing of individual pups?*” (Q2) and “*when the focal pup is vocalising, does the*
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59 156 *presence of a silent partner (vs. no partner) affect call timing?*” (Q3). We answer these questions
60
157 using circular statistics (Q2 and Q3) and Granger causality tests (Q2). Lastly, ADAM is used to
158 investigate the fourth question about the cognitive processes involved in temporal adjustment: “*which*
159 *timing mechanisms are used by pups during vocal interactions?*” (Q4).

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4 161 **1.5. Subjects, housing conditions, and behavioural contexts**

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6 163 We recorded nine wild-born pups (A-I) calling in different behavioural contexts while housed
7 164 at Sealcentre Pieterburen (the Netherlands) (Method S1/S2). During the recordings, each pup was
8 housed in an enclosure with a swimming pool and a resting platform (Figure S1). One pup was housed
9 165 alone (I) while the others were housed in pairs (A/B, C/D, E/F, G/H). Note that the enclosures were
10 166 physically but not acoustically isolated from each other, meaning that pups could hear other pups in
11 167 neighbouring enclosures.

12 168

13 169 We analysed focal pup vocalisations during four different behavioural contexts (Figures 1, Table
14 170 S1): (i) when the focal pup was alone (pup I), (ii) when the focal pup heard a playback of conspecific
15 171 calls (pup I), (iii) when the focal pup's partner was silent (pups A-H), and (iv) when the focal pup's
16 172 partner was also vocalising (pups A-H). Hereafter, we refer to these conditions as: (i) alone, (ii) 1-
17 173 way interaction with a broadcasted partner, (iii) silent partner, and (iv) 2-way interaction with a real
18 partner. Notice that only some pups entered each condition and vice-versa (Table S1).

19 174

20 175 Our sample size was affected by the unpredictable arrival of animals at the Sealcentre, which
21 176 varies seasonally. Only medically stable and healthy pups were included in this study. The number of
22 177 daily recording sessions per pup pair varied based on veterinary staff recommendations at the
23 178 rehabilitation centre (Table S1); we did not record pups with signs of disease. Data from pup I (i.e.,
24 179 the alone and 1-way contexts both with and without playback stimuli) have been re-analysed from
25 180 previous studies [28,21, respectively] and combined with unpublished data from pups A-H (the silent
26 181 partner and 2-way contexts) (Table S1). The contribution of each pup to each analysis is shown in
27 182 Table S2.

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30 185 **1.6. Extraction of temporal variables, definition of call bout and vocal interactions**

31 186

32 187 We first extracted the onsets and offsets of each pup call recorded in each behavioural context
33 188 (Figure 1, Method S3). From these values, we calculated rhythmic metrics such as call duration, inter-
34 189 onset intervals (IOIs), ratios of adjacent IOIs, and inter-call intervals (ICIs; i.e., silent gaps). Each IOI
35 190 was obtained by subtracting the *onset* of call n from the *onset* of call $n+1$, while the ICI was calculated
36 191 by subtracting the *offset* of call n from the *onset* of call $n+1$ (i.e., IOI minus duration of call n). Calls
37 192 were organised into bouts, defined here as a series of at least three subsequent calls that were separated
38 193 from adjacent bouts by a period greater than 1.5 times the median ICI of the recorded individual(s)
39 194 calls (Figure 1). The response phase was computed as the ratio of the 'response IOI' (i.e., time interval
between the call onset of the partner and the call onset of the pup's response) and the previous IOI,
multiplied by 360, resulting in a unit vector with an angle on a circle. A vocal interaction was defined
as a group of three calls within the same bout, which includes two calls from the broadcasted/real

partner followed by the response of the focal individual (Figure 1). Following previous methodology [28,38], we calculated the IOI ratio, r_k , for each pair of adjacent IOIs, t_k and t_{k+1} , in a bout as:

$$r_k = \frac{t_k}{t_k + t_{k+1}}$$

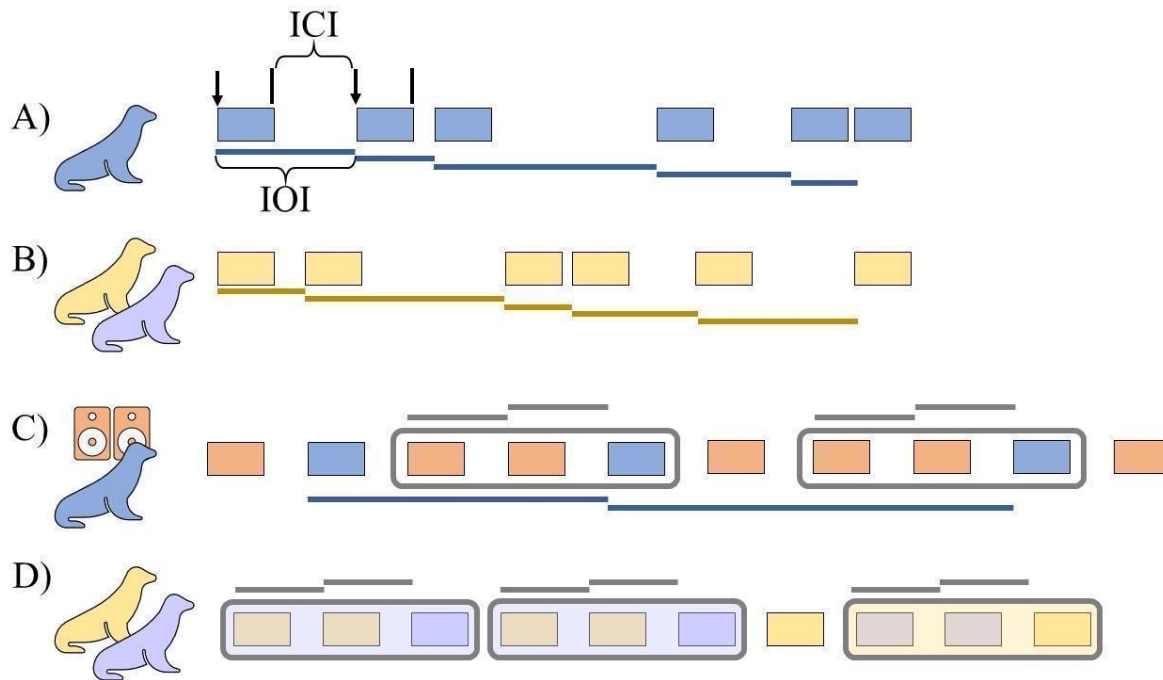


Figure 1. Schematic of experimental conditions and key measurements. Each of the four rows represents one bout and indicates a different behavioural context: (A) alone, (B) silent partner, (C) 1-way interaction, and (D) 2-way interaction. Boxes are coloured to represent the call source and grey rectangles denote vocal interactions. For bouts (C) and (D), calls are isochronously spaced for ease of visualisation, but empirical patterns were not necessarily isochronous. Horizontal bars indicate how IOIs were calculated for different analyses. The call onsets (black arrows) and offsets (black lines) are shown for the first two calls in (A).

1.7. Descriptions of analytical approaches

Circular statistics, wherein periodic measures are converted to angles on a circle and compared to distributions of interest [40], were used to investigate rhythmic periodicities in pup call response phases (Method S4). Following [21], we considered the values of the response phases as circular data falling between 0° and 360° . We obtained the circular mean (μ) (i.e., the average direction of the response phases calculated from the pup calls; Table S3). Then, we ran Rayleigh z-tests to investigate whether the distribution of response phases was uniform (e.g., arousal hypothesis) or showed a unimodal peak (Table S4) [21]. Subsequently, we tested for uniformity against a specified mean direction for the unimodal peak using a V-test [40–43].

Our data met the assumptions for circular statistics. We tested if the response phases in all four behavioural contexts followed a von Mises distribution using one-sample Watson tests (Table S5). With deviations from uniformity (null hypothesis von Mises distribution rejected), we used Kuiper's

1
2 221 test, Watson's test, and Rao's spacing test, to confirm the p-value obtained from the Rayleigh test
3
4 222 (Table S6) as suggested by Landler et al. [40]. More details are shown in Method S4.

5 223 We then tested whether response phase distributions varied depending on the presence of the
6
7 224 calling partner. We expected that vocally interacting pups would adjust their responses to broadcasted
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9 225 (1-way interaction) or real (2-way interaction) conspecific calls to avoid overlap and, hence, their
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11 226 response phases would show a unimodal distribution. Following previous work [21] and applying the
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13 227 V-test, we tested the null hypothesis of call response phase uniformity against two alternative
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15 228 unimodal departures: 0° (i.e., synchrony) and 90° (i.e., asynchrony). Using Watson's two-sample U^2
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17 229 test [44], we also compared the call phase distributions of 1) a pup calling alone vs. when responding
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19 230 to a broadcasted partner (pup I) and 2) a pup calling in the presence of a silent partner vs. when their
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21 231 partner was also calling (pups A-H). For interacting (1-way or 2-way) pups, we applied Watson's two-
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23 232 sample U^2 test to assess whether the type of partner (i.e., real or broadcasted) differentially affected
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25 233 the pups' response timing. We predicted that pups interacting with a real partner would show more
26
27 234 adaptive call timing, thanks to potential communicative cues from other modalities. Lastly, we
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29 235 compared the distributions of call phases of the single pup vocalising alone to those of the paired pups
30
31 236 when their partner was silent to test whether the simple presence of a silent partner affects individual
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33 237 call timing. In both behavioural contexts, we predicted that calling patterns for pups without a
34
35 238 responsive partner would show a different rhythmic structure to those observed in interaction.

36
37 239 **Categorical rhythm** analysis tests whether the temporal intervals between signal onsets, as
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39 240 inferred from IOI ratios, are distributed categorically rather than uniformly. We predicted that
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41 241 empirical and simulated null ratio distributions (i.e., the expected distribution if no rhythmic
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43 242 categories exist) will not differ when a pup is alone or with a silent partner but will differ when a pup
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45 243 is vocally interacting. For vocally interacting pups, we predicted a significant peak in empirical ratio
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47 244 distributions at the 4:1 small integer ratio based on the lone seal in [21], which called at approximately
48
49 245 one-quarter of the playback's period. All categorical rhythm analyses were done within bouts
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51 246 following previous methodology (section Method S5) [23,24], with IOIs calculated in various ways
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53 247 depending on the behavioural context (Table S8, Figure 1). We used one-sample Kolmogorov-
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55 248 Smirnov (KS) tests to determine whether empirical IOI ratio distributions significantly differed from
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57 249 simulated null IOI ratio distributions. Our data met the one-sample KS test assumptions, namely that
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59 250 the sample is random and the theoretical distribution is continuous and fully defined. When the
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61 251 empirical and simulated distributions were significantly different, we also looked for evidence of
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63 252 small integer ratio (SIR) categorical rhythms—specifically at the 1:4, 1:3, 1:2, 1:1, 2:1, 3:1, and 4:1
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65 253 ratios—which have been found in other species' vocalisations [23,24]. In these analyses, the empirical
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67 254 ratio distributions were divided into “on-integer” and “off-integer” ratio bins (Table S7). On- and off-
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69 255 integer bin counts for each SIR were normalised by bin size and compared using a paired Wilcoxon

1
2 256 signed-rank test (a non-parametric test that allows for non-normality in the population data and
3
4 257 assumes paired differences are continuous, symmetrically distributed, and mutually independent).
5
6 258 When sample sizes allowed, we used two-sample KS tests (having met the assumption of mutual
7
8 259 independence of measurements within samples) to determine whether the ratio distributions of
9
10 260 individual pups differed across behavioural contexts.

11 261 The **Granger causality** test investigates whether the values of a time series A are better
12 262 predicted when considering the values from a second time series B, as opposed to only using values
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14 263 from time series A [45]. Here, we assessed whether the call timing of a pup partaking in a 1-way or
15
16 264 2-way vocal interaction can be predicted using the call timing of its partner. More specifically, to
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18 265 investigate whether the call timing of a pup differed in relation to the type of partner, we tested
19 266 whether there is a difference in predicting the time series of the pup interacting with a broadcasted
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21 267 partner vs. time series of the pups interacting with a real partner. Previous work showed that
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23 268 individuals respond to conspecific calls with a non-random pattern [18–20,46]. We therefore expected
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25 269 that the time series of a pup can be better predicted considering the time series of a vocalising partner
26 270 rather than those of a broadcasted signal. In both the 1-way and 2-way interactive scenarios, we
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28 271 considered Granger causality at two levels: (1) the entire recording, regardless of the length of the
29
30 272 pauses between consecutive calls, and (2) different bouts within each recorded session. **We restricted**
31 273 **the analysis on the different bouts to call sequences that were long enough to generate accurate**
32
33 274 **estimates (i.e., a minimum of five paired calls [47]). The bouts included in this analysis range from 5**
34
35 275 **to 20 calls.** We conducted the Granger causality test using call onsets and different *lag* measures, from
36
37 276 one to five (Method S6), testing whether the previous one to five onsets in the first time series can be
38 277 used to better predict the second time series (Figures S5/S6, Table S11). For the 1-way interaction,
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40 278 we performed a one-way analysis, considering whether the pup's timing could be predicted using the
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42 279 playback timing. For the 2-way interaction, we performed a two-way analysis to assess whether the
43 280 two interacting pups influenced the timing of each other's calls.

45 281 We used **ADAM** to test for evidence of reactive error correction and predictive processes in the
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47 282 1-way and 2-way interactive scenarios. ADAM consists of three computational modules that interact
48
49 283 via internal models of 'self' and 'other' that support one's own action planning and external event
50 284 prediction, respectively (Figure S2). The *adaptation module* compensates for synchronisation errors
51
52 285 by implementing error correction processes that alter the phase and/or period of an internal timekeeper
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54 286 controlling for action (here, call) timing. These error correction processes determine the provisional
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56 287 timing of the next planned action by providing input to an internal model of the 'self'. The
57 288 *anticipation module* computes the expected timing of upcoming events based on the weighted sum
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59 289 of two processes: the linear extrapolation of previous IOIs in the sequence and the copying (or
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290 'tracking') of the previous IOI, with the output informing temporal predictions generated by the

1
 2 291 ‘other’ internal model. Finally, a *joint module* integrates and compares the output of the adaptation
 3
 4 292 and anticipation modules and compensates for discrepancies by implementing an anticipatory error
 5
 6 293 correction process before the next motor command is issued. The joint module thus reduces potential
 7
 8 294 temporal mismatches between action plans in ‘self’ internal models and temporal predictions in
 9
 10 295 ‘other’ internal models, thereby regulating the balance between the integration (merging) and
 11
 12 296 segregation (distinction) of information about ‘self’ and ‘other’ [48,49]. Each process instantiated in
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 14 297 ADAM is controlled by an independent parameter, and the value of these parameters can be estimated
 15
 16 298 for a particular individual by fitting the model to behavioural time series data [26,27,50,51].
 17
 18 299 Parameter estimates were obtained for both the adaptation-only version of ADAM—which includes
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 20 300 phase correction and period correction—and the full (‘joint’) version—including period correction,
 21
 22 301 temporal prediction/tracking, and anticipatory error correction. Both versions of ADAM were applied
 23
 24 302 to each interactive context because it is not possible to know a priori whether the pups’ call sequences
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 26 303 (real or broadcasted) have a steady base tempo (for which adaptation is sufficient) or a systematically
 27
 28 304 changing tempo (which benefits from both anticipation and adaptation) (Method S7).
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38 **Table 1.** Summary table showing in order: research questions, analyses, contributing pups, predictions,
 39 whether the data supports each prediction, statistical test(s) used, and result(s) obtained. The column
 40 “Supported by data?” has three possible answers: results support the prediction (Y), results only partially
 41 support the prediction (Partial), and results do not support the prediction (N). Due to sample size and/or
 42 analytical requirements, not all pup data could be used in each analysis. The acoustic variables of interest for
 43 the different analytical approaches were: response phases (circular statistics), IOI ratios (categorical rhythms),
 44 IOIs (Granger causality, ADAM), and asynchronies (ADAM).
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Research question	Analytical approaches	Pups	Prediction	Supported by data?	Statistical test(s) and result(s)
Temporal domain, Q1: <i>Does the presence of a calling partner affect the call timing of individual pups?</i>	Circular statistics	A-I	Pups will not vocalise at random points in time.	Y	Rayleigh test: Unimodal distribution of response phases.
			Pups will call in asynchrony to avoid overlap during vocal interactions.	Y	V-test: Pup calls start at one-quarter of the partner’s period
			Response phases will be affected by the presence of a vocalising partner.	Y	Watson’s U ² test: Response phase distributions differ between non-interactive and interactive contexts.

	Categorical rhythms	A, B, C, E, H, I	Empirical and chance ratio distributions will only significantly differ when pups are vocally interacting.	Partial	1-sample KS tests: Simulated and empirical ratio distributions are rarely significantly different (exceptions: pup I alone, pup I 1-way, pup B 2-way).
		A, B, I	Vocally interacting pups will have a significant peak at the 4:1 SIR.	N	Paired Wilcoxon signed-rank test: No significant peaks at any of the tested small integer ratios.
			Ratio distributions of individual pups will differ across behavioural contexts.	Y	2-sample KS tests: Ratio distributions significantly differed for the same individuals in different behavioural contexts.
Social domain, Q2: Does the type of calling partner (real or broadcasted) affect the call timing of individual pups?	Circular statistics	A-I	Pups interacting with a real partner will show more adaptive call timing than the pup interacting with a broadcasted partner.	N	Watson's U^2 test: No difference in response phases between 1-way and 2-way interactions.
	Granger causality	A, B, C, D, E, F, I	The time series of a pup will be better predicted considering the time series of a vocalising partner rather than the time series of a broadcasted signal.	Y	Bidirectional & unidirectional causality: Interaction with a real partner impacted the pup's vocal behaviour more than the playback. Mutual temporal adaptation among pairs of vocally interacting pups.
Social domain, Q3: When the focal pup is vocalising, does the presence of a silent partner (vs. no partner) affect call timing?	Circular statistics	A-I	The calling pattern of pups will show similar rhythmic structure in both the alone and silent partner conditions, as no vocal interaction is taking place in both cases.	Y	Watson's U^2 test: No difference between response phase distributions of pup calling alone and pups calling with a silent partner.

<p><i>Cognitive domain, Q4: Which timing mechanisms are used by pups during vocal interactions?</i></p>	ADAM	A, B, I	<p>In the 1-way interaction, pups may show sensitivity to (non-)interactivity which would be reflected by parameter changes over repeated sessions. The 2-way interaction may be mediated by basic temporal adaptation and possibly higher-level anticipatory timing.</p>	Partial	<p>1-way interaction: Temporal anticipation, and to a lesser extent also adaptation, decreased across the playback sessions, and was absent in the final session. 2-way interaction: Clear evidence for temporal adaptation, with differing parameter estimates for each seal pup suggesting the emergence of different interactive roles.</p>
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3. Results

3.1. Does the presence of a calling partner affect the call timing of individual pups? (Q1)

All pups' data entered the circular statistics analysis. Running the Rayleigh test, we found that the response phase distribution was uniform for **pup I** which was recorded alone ($z = 0.04$, $p = 0.254$; Figure 2A), whereas it was non-uniform for **pups A-H** which were recorded with a silent partner ($z = 0.11$, $p < 0.001$; Figure 2A; Table 1). This non-uniformity may have been driven by the individual contributions of **pups B** and **C**, which had non-uniformly distributed response phases (Table S4), whereas the other **six pups** had a uniform distribution. The Rayleigh tests run anew in the interactive contexts, showed that the response phase distributions of pup calls were unimodal in both the 1-way (**pup I**: $z = 0.39$, $p < 0.001$) and 2-way (**pups A - H**: $z = 0.41$, $p < 0.001$) interactions (Figure 2B; Table 1). Applying the V-test in both contexts, the direction of the response phases did not statistically match 0° (1-way: $z = -0.02$, $p = 0.587$; 2-way: $z = 0.06$, $p = 0.110$), suggesting that pups did not synchronise with their partner (real or broadcasted). However, the response phase direction did match 90° (1-way: $z = 0.38$, 2-way: $z = 0.41$, $p < 0.001$), supporting the previously reported evidence of asynchronous calling behaviour [21]. A Watson's two-sample U^2 test confirmed that the response phase distributions significantly differed between the alone vs. 1-way interaction context for **pup I** ($U^2 = 1.76$, $p < 0.001$), and between the silent partner vs. 2-way interaction context for **pups A-H** ($U^2 = 0.78$, $p < 0.001$, Figure S3; Table 1). Finally, the circular standard deviation values were higher for the alone and silent partner contexts compared to both interactive vocal contexts, indicating a larger dispersion of the response phases for the former conditions. This outcome is also confirmed by the values for the mean resultant length.

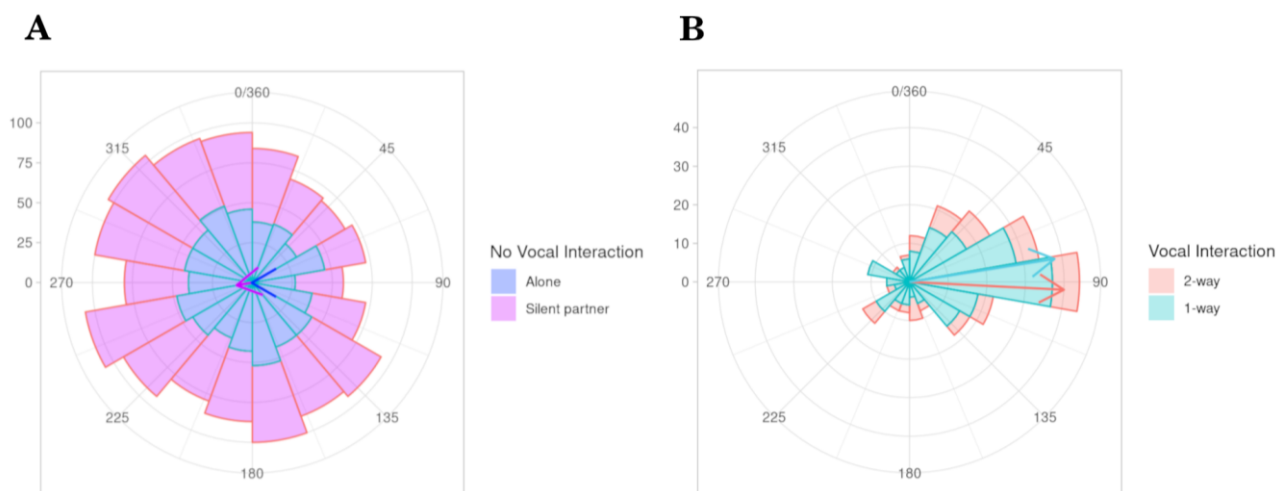


Figure 2. Circular histogram plots (bin width = 20°) showing response phases in (A) both types of behavioural contexts with no vocal interaction (alone/silent partner), and (B) in both types of vocal interaction contexts (1-way/2-way). Angles are measured in degrees starting from 0° and going clockwise to 360°. The arrows indicate the circular mean (μ) and colours correspond to the different behavioural contexts. The length of the arrow corresponds to the value of the mean resultant length (ρ).

In the categorical rhythm analyses, the empirical ratio distribution was significantly different from chance when **pup I** was recorded alone (Figure 3A) and during the 1-way interaction (Figure 3C). In both contexts, there was no evidence of significant peaks at any of the tested ratios (Table 1). When the playback calls were disregarded from IOI calculations (Figure 3B), there was no significant difference in empirical and simulated ratio distributions for **pup I**. However, pairwise KS tests showed that the ratio distributions significantly differed when comparing each of the three behavioural contexts (alone vs. 1-way interaction disregarding playback vs. 1-way interaction when **pup I** responds) to each other (Table S10; Table 1). For the **five pups** that were well-sampled in the silent partner context (**pups A, B, C, E, and H**; Table S8), the empirical ratio distributions did not significantly differ from chance (Table S9, Figures 3/S4, Method S4). Finally, when considering 2-way interactions, only **pups A and B** were well-sampled enough (i.e., had at least ten ratios for both the silent partner and 2-way interaction contexts) to compare, but the empirical and simulated ratio distributions were significantly different only when **pup B** was the responder (Figure 3; Table S8; Table S9). Once again, there were no significant peaks at any of the tested ratios for **pup B**. For both **pups A and B**, the empirical ratio distributions significantly differed when comparing different behavioural contexts (Table S10). Collectively, there was thus little evidence of SIR rhythmic categories in pup calls, but IOI ratios did significantly differ when looking at the same individuals in different behavioural contexts (Table 1).

Thus, the results from both analyses suggest that the *presence* of a calling partner does affect the call timing of the focal pup, in terms of both call response phases and IOI ratios.

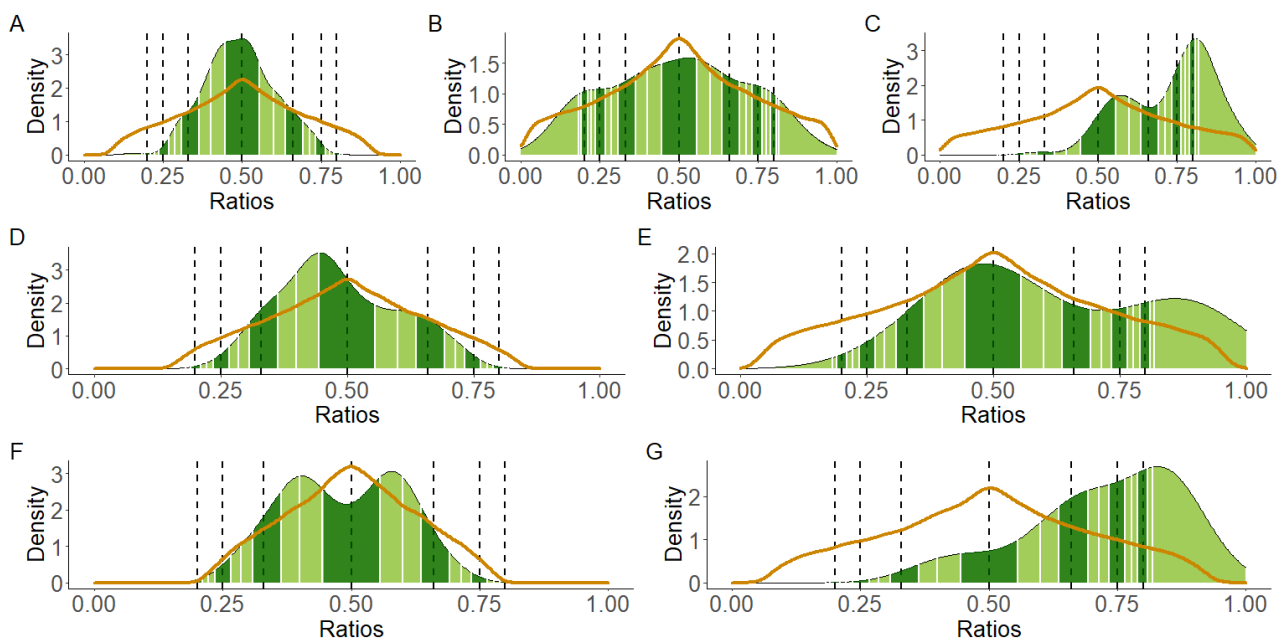


Figure 3. IOI ratio density plots for pups in different behavioural contexts. **Pup I:** (A) alone, (B) 1-way interaction (disregarding playback), (C) 1-way interaction (responding to playback). **Pup A:** (D) silent partner, (E) 2-way interaction (responding to partner). **Pup B:** (F) silent partner, (G) 2-way interaction (responding to partner). For each plot, the dashed vertical lines indicate, from left to right, 1:4, 1:3, 1:2, 1:1 (i.e., isochrony), 2:1, 3:1, and 4:1 small integer ratios. On-integer ratio ranges are in dark green and off-integer ratio ranges are in light green, with white lines and black dashed lines denoting bin boundaries. The orange curves indicate the ratio distribution expected under a uniform distribution if no rhythm categories exist. The empirical ratio distribution significantly differed from the simulated ratio distribution for panels (A), (C), and (G) only. Note that the scale of the y-axes differ.

3.2. Does the type of calling partner (real or broadcasted) affect the call timing of individual pups? (Q2)

To address this research question, we once again used circular statistics and the response phase distributions of **all nine pups**. Specifically, we compared calls from **pup I** during the playback (1-way interaction) with calls of **pups A-H** when their partner was also calling (2-way interaction). A Watson's two-sample U^2 test statistically confirmed that the response phase distributions did not differ between the 1-way and 2-way vocal interactions ($U^2 = 0.07$, $p > 0.10$; **Table 1**).

Interestingly, however, the Granger causality results from **seven pups (A, B, C, D, E, F, I)** showed that call timing behaviour differed depending on the type of partner (**Table 1**). For the 1-way interaction, five different playback sessions featuring **pup I** were considered (ranging from 34 to 121 paired calls) and the timing of the pup's calls were never significantly predicted by the timing of the playback (**Table S11**, **Figure S5**). For the 2-way interaction, five different recording sessions were considered (ranging from 8 to 71 paired onsets). We found that in two sessions, the timing of the first pup did not significantly predict the timing of the second, in either direction (**pair A>B and B>A; pair E>F and F>E**; **Table S11**, **Figure S6B/S6D**). However, in two other sessions, the timing of a pup was significantly predicted by the calling partner in both directions, across different lag values (A>B: lag-

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 2 392 1, lag-3, lag-4, lag-5; B>A: lag-3, lag-4, lag-5; C>D and D>C: lag-2 and lag-3; Table S11, Figure
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 4 393 S6B/S6C). In the last session, the timing of **pup A** could be predicted by that of **pup B**, while we found
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 6 394 no indication of temporal adjustment for **pup B**. At the bout level, we restricted our analyses to four
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 8 395 series of paired onsets featuring **pups A and B** (as they were the only pup pair that met the sample
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 10 396 size requirements). In this last scenario, only the timing of **pup B** was significantly influenced by **pup**
 11 397 **A** (Figure S6A).

12 398 While the circular statistics results thus suggest that the type of calling partner (real vs.
 13
 14 399 broadcasted) does not affect focal pup call timing, the Granger causality results suggest that in certain
 15
 16 400 2-way (but not 1-way) interactions, focal pup call timing can be predicted by the partner's call timing.

17 401 18 19 402 **3.3. When the focal pup is vocalising, does the presence of a silent partner (vs. no partner)** 20 21 403 **affect call timing? (Q3)**

22
 23 404 Using circular statistics, we compared the calls of **pup I** recorded alone with those of the **8 other**
 24
 25 405 **pups (A-H)** recorded with a silent partner present. Watson's two-sample U^2 test results show that the
 26 406 response phase distributions did not statistically differ between the two contexts ($U^2 = 0.10, p > 0.05$).
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 28 407 In other words, having a silent partner was essentially the same as having no partner—in terms of the
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 30 408 effect on focal pup response phase distributions—for the pups in our study. This is intuitive, given
 31 409 that in both behavioural contexts, there is no acoustic stimuli to “respond” to.
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33 410 34 35 411 **3.4. Which timing mechanisms are used by pups during vocal interactions? (Q4)**

36 412 ADAM parameter estimation was conducted on call data from all five playback sessions
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 38 413 featuring **pup I** (1-way, Figure 4 A/B), but was restricted to **pups A and B** for the 2-way interactions
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 40 414 due to sample size limitations (Figure 4 C/D). Interactive vocal bouts were concatenated to obtain a
 41
 42 415 time series length which would provide reliable ADAM parameter estimates. A simulation test then
 43 416 ensured that the estimates were not compromised by differing sequence lengths or by the
 44
 45 417 concatenation procedure (Method S7). The reliability of observed parameter estimates was tested by
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 47 418 comparison against corresponding values for randomly permuted data (Method S7). The quality of
 48
 49 419 the fits to the data did not differ significantly between versions of ADAM (Method S7). Results for
 50 420 the 1-way interaction featuring **pup I** were remarkable with regards to typical human data (e.g.
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 52 421 [26,27]) as most significant parameters were negative in sign (**Figure 4A/B, Tables S13/S14**).
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 54 422 Negative phase and period correction estimates indicate that calling earlier will lead to a shortening
 55
 56 423 of the next IOI, while calling later will lead to a lengthening of the next IOI. Negative
 57 424 prediction/tracking estimates mean that when the playback's IOIs increase (i.e., deceleration), the
 58
 59 425 pup's IOIs will decrease (i.e., acceleration), and vice versa. This systematically enhances the timing
 60 426 distinction between calls, possibly testing the responsiveness of the partner (i.e., playback) by

introducing timing asynchronies and gauging their effects. It is worth noting that evidence of such behaviour generally decreased across the five playback sessions, with no significant parameter estimates emerging in the final session.

For the 2-way interaction (Figure 4C/D, Tables S13/S14), the parameter estimation procedure was run twice, each time with one of the two pups serving as the focal individual and the other as the external reference. With this procedure, similar parameter estimates for each pup would indicate a symmetrical pattern of influence, whereas different estimates would indicate asymmetrical influence. Results for this type of vocal interaction showed evidence for temporal adaptation. In particular, parameter estimates were consistent with pup A engaging in period correction while pup B engaged in both phase and period correction. Period correction estimates were positive in sign for pup A and negative for pup B. Pup A's positive period correction estimates suggest that calling earlier will lead to a lengthening of the next IOI, whereas calling later will lead to a shortening of the next interval. Pup B exhibited the opposite effect but to a lesser degree. Pup A thus implemented a timing mechanism that increased the similarity in their calling rates, while pup B implemented a timing mechanism that increased the distinction in calling rates. It should be noted, however, that the observed parameter estimates do not necessarily reflect individual call styles per se, but rather the roles that dynamically emerge within the context of this specific pairing of pups.

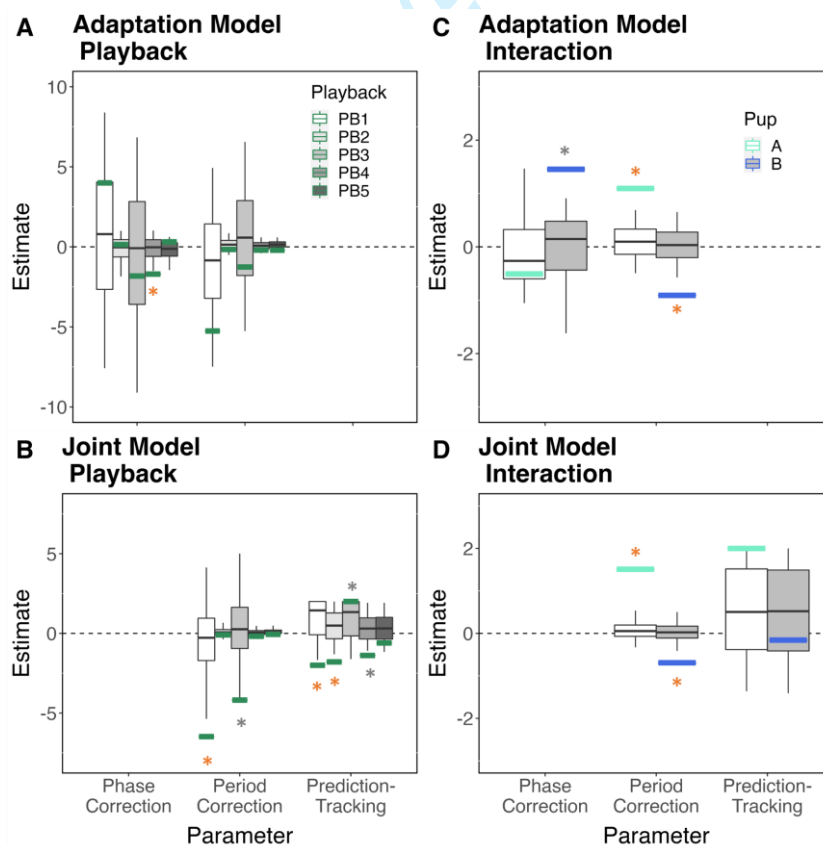


Figure 4. ADAM parameter estimates for seal pups **A, B, and I**. Left panels (A & B) show parameter estimates for **pup I** in five playback sessions (1-way interaction); right panels (C & D) show estimates for **pups A and B** (2-way interaction). Top panels (A & C) show phase correction and period estimates obtained with the adaptation-only version of ADAM; bottom panels (B & D) show period correction and prediction-tracking estimates for the full 'joint' model (anticipatory error correction estimates are not shown). Parameter estimates are shown separately for **pup A** relative to **pup B** (aquamarine bars) and **pup B** relative to **pup A** (blue bars) in the recording session, and for **pup I** (green bars) relative to playback calls in separate playback sessions (PB1-PB5). Corresponding parameter estimates for randomly permuted data from each session are represented by box plots, with the central horizontal line indicating the median, the bottom and top edges of the box indicating the 25th and 75th percentiles, and the whiskers indicating the 5th and 95th percentiles. Real estimates with asterisks are significantly different from permuted data estimates at the 2-tailed (orange) or 1-tailed (grey) level.

4. Discussion

This study sought to provide a methodological proof of concept for quantifying vocal rhythmicity in non-human animal interactive communication. Particularly, we showed how complementary methodologies can be used to test whether the (Q1) presence and (Q2) type of a vocalising partner, or the (Q3) presence of a silent partner affect patterns in animal communication (Table 1). We also investigated which (Q4) underlying cognitive mechanisms potentially play a role in vocal interactions (Table 1). The different analytical techniques proved fruitful; combining and contrasting their results could highlight nuances in rhythmic behaviour. Nonetheless, our sample size is undeniably small, and our opportunistic design (e.g., mixing within- and between-individual comparisons) cannot provide strong inference. We believe that our experimental setup, combined with the approaches we present, can be adapted and expanded in future work to better understand the temporal, social, and cognitive processes underlying interactive communication in animals.

Q1. The presence of a vocalising partner influences rhythm in vocal interactions

The prediction of overlap avoidance was supported by circular statistics, which showed that the distributions of response phase angles were unimodal. When vocally interacting, pups responded at approximately one-quarter of the playback/real partner calling period (90°) and showed phase angles significantly different from 0° , supporting previous results from one individual (**pup I**) [21]. Pups responding to conspecifics seem to time their calls to avoid overlap, consistently de-synchronizing their call onsets. When pups were recorded alone or with a silent partner, the distribution of phase angles was uniform, with no significant rhythmic pattern. Our findings confirm and extend previous outcomes [21]; in our limited sample, pups not only react to playbacks with asynchrony, but also respond to conspecific partner calls in an asynchronous manner.

Regarding categorical rhythms, the empirical ratio distribution did not significantly differ from the distribution expected by chance if IOIs were uniformly distributed for most pup/behavioural context combinations (7/10). For the remaining three combinations (**pup I** alone; **pup I**, 1-way interaction; **pup B**, 2-way interaction), there was no significant evidence that call timing exhibited

1
2 487 categorical rhythms at the seven tested small integer ratios. This includes the 4:1 ratio, which we
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4 488 hypothesised would frequently occur when pups were vocally interacting with playback stimuli or
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6 489 partners based on previous work [21]. Importantly, however, the empirical ratio distributions
7 490 significantly differed across behavioural context conditions for the three pups (A, B, I) for whom such
8
9 491 comparisons were possible. When alone or with a silent partner, pup calls generally showed unimodal
10
11 492 ratio distributions centred around isochrony, whereas calls emitted by vocally interacting pups
12 493 showed a clear right-shifted peak, or a second peak to the right of isochrony, indicating that the pup's
13
14 494 IOIs during vocal interactions were generally shorter than the playback's/partner's IOIs. This context-
15
16 495 dependent asymmetry bolsters results related to Q4, namely that the presence of vocalising partner
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18 496 can significantly impact pup vocal behaviour, with interacting individuals trying to prevent call
19 497 overlap. Roeske and colleagues [23] hypothesised that categorical rhythms may be prevalent in calls
20
21 498 meant to attract and hold conspecific attention, such as the calls pups use to attract the attention of
22
23 499 their mothers. We did not find evidence of rhythm categories at seven tested ratios; this negative result
24
25 500 has methodological value, highlighting that not all species that produce attention-seeking
26 501 vocalisations show integer ratio categories.

27
28 502 A vocal interaction with non-adaptive playback stimuli (1-way) may represent a limitation to
29
30 503 studying spontaneous vocal production. The extent of this limitation can be gauged by comparing
31 504 results to data from vocal interactions with a real partner (2-way), and with the use of complementary
32
33 505 analytical methodologies, such as categorical rhythm analysis and circular statistics.

36 507 **Q2. Type of calling partner (real or broadcasted) partly affects rhythm in interaction.**

38 508 Findings from Q2 show contrasting results. Call phases were statistically the same no matter if
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40 509 pups could interactively adjust their call timing to each other (2-way) or not (in 1-way). Partly in
41
42 510 contrast with this, the Granger causality analysis showed how vocally interacting with a real
43 511 individual impacted the pup's vocal behaviour more than interacting with a broadcasted partner
44
45 512 Indeed, we found evidence of mutual temporal adaptation among pairs of vocally interacting pups
46
47 513 and, consistent with a recent hypothesis [6], conspecific interactions can be facilitated by the
48
49 514 reciprocal adjustment of timing behaviour. In contrast, we found little evidence that a pup adjusts the
50 515 time series of its calls to a playback series. Indeed, in most cases, the pup's call timing could not be
51
52 516 predicted by the playback's call timing.

53
54 517 Together, findings from circular statistics (Q1) and Granger causality (Q2) point towards a
55 518 directionality-overlap avoidance relationship, which has also been suggested for other non-human
56
57 519 species (e.g., primates [18,52]; birds [53]; amphibians [54]; seals [55]). **Interestingly, when infant**
58
59 520 **marmosets interact with their parents, the probability that their vocalisations will overlap with those**
60

1
2 521 of adults decreases over time [22], suggesting that turn-taking in some mammals is a learned vocal
3
4 522 behaviour scaffolded by active parental feedback [39].
5
6 523

7 524 **Q3. A silent partner does not trigger call rhythmicity**

8
9 525 Circular statistics indicated that pups did not show any periodic pattern both, either when calling
10
11 526 alone or with a silent partner present (Q1). This is consistent with the fact that wild pups produce calls
12
13 527 to attract a silent mother [36]: if no other calling conspecifics are present, there is no need to adjust
14 528 one's call timing and vocalisations are produced with a random onset. Moreover, given that the
15
16 529 response phase distributions did not differ between pups recorded with a silent partner or alone, it
17
18 530 suggests that the presence of a silent partner did not trigger variable calling behaviour in our study
19 531 population.
20
21 532

22 23 533 **Q4. Purported timing mechanisms for vocal interactions**

24 534 The ADAM analysis suggests that seal pups may perceive temporal patterns [56], which arise
25
26 535 between their calls and those of others, and react to them by adopting different mechanisms for
27
28 536 temporal adaptation. The negative parameter estimates that we observed in the 1-way interaction
29
30 537 sessions (consistent with enhancing the distinction between calls) could reflect attempts to lead the
31
32 538 temporal interaction or even to test the responsiveness of the (broadcasted) partner by introducing
33 539 timing perturbations and gauging their effects. The decrease of temporal adaptation and/or
34
35 540 anticipation observed across playback sessions is consistent with a gradual process of habituation,
36
37 541 with the pup possibly learning that the playback is non-interactive. Harbour seals are capable of
38 542 acoustic recognition based on habituation paradigms; they can discriminate among different stimuli
39
40 543 and selectively habituate to them [57]. The lack of temporal adaptation to the playback stimulus we
41
42 544 observed in a seal pup may entail similar habituation processes. From a comparative perspective,
43 545 these findings also suggest a sensitivity to social contingency that may be analogous to capacities in
44
45 546 human infants, who become disinterested and display fewer signs of positive affect during vocal
46
47 547 interactions with non-responsive or delayed video recordings of their mothers [58–62]. Future studies
48
49 548 could address the role of temporal contingency by using interactive playback sequences [63–65].

50 549 Ours constitutes the first attempt to apply ADAM to non-human animals. On the technical side,
51
52 550 this necessitated the validation of an approach where brief interactive vocal bouts were concatenated
53
54 551 to produce longer time series and thereby reduce the risk of model overfitting (Discussion S1).
55 552 Demonstrating the utility of this procedure opens the door to applying the model in a wider range of
56
57 553 behavioural contexts. Nevertheless, caveats are necessary when interpreting the seal data in light of
58
59 554 previous work with ADAM in humans, where individuals intentionally produce movements, whose
60
555 sensory effects occur simultaneously with rhythmically regular sounds (e.g. [26,27]). Assumptions

1
2 556 about intentionality and simultaneity may not apply to seal pup vocal interactions or rhythmic
3
4 557 interactions in other animals [6,9]. Points of convergence in the main outcomes of the complementary
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6 558 analysis techniques suggest that ADAM, like categorical rhythm analysis, circular statistics, and
7
8 559 Granger causality, may also be robust and informative under such conditions.
9
10 560

11 561 **5. Conclusions**

12 562 Crucially, our work highlights the efficacy of combining multiple methods to study rhythmic
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14 563 vocal behaviour. Our approaches vary in the degree to which they capture global temporal
15
16 564 characteristics across events vs. local temporal dependencies between events. Global measures (e.g.,
17
18 565 from circular statistics or categorical rhythm analysis) reveal predominant rhythmic features of a
19
20 566 vocal interaction while local time series measures (e.g., from Granger causality or ADAM) provide
21
22 567 information about how these features might arise. Through this approach we could tease apart rhythm
23
24 568 nuances in our dataset, further develop harbour seals as a model species, and demonstrate how certain
25
26 569 analyses often restricted to humans, such as categorical rhythms (but see [23,24]) and ADAM, can be
27
28 570 applied to non-human animals. The categorical rhythm and circular statistical analyses tackled similar
29
30 571 questions from different angles, namely whether the distributions of IOI ratios (the former) or call
31
32 572 response phases (the latter) significantly differed across behavioural contexts. The categorical rhythm
33
34 573 analyses also sought to determine whether the rhythmicity of pup calling behaviour conforms to small
35
36 574 integer ratios. Our negative result is, to our knowledge, the first published case of a species for which
37
38 575 categorical rhythms are clearly absent from vocalisations, which adds to understanding of how, why,
39
40 576 and when such rhythms evolve in communication systems. Time series analyses such as Granger
41
42 577 causality allowed testing for timing adjustment. In the case of ADAM, mechanisms of temporal
43
44 578 adaptation and anticipation that have previously been used to describe rhythmic behaviour in humans
45
46 579 [66] were used to describe rhythmic behaviour in seals. Interestingly, the ADAM model provides an
47
48 580 empirical warning about potential seal pup habituation effects when vocally interacting with a
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50 581 recorded partner.

51
52 582 **Though our sample size is small, studies on single individuals are not unusual in comparative**
53
54 583 **research [20,67]. Nevertheless, it is possible that the lack of adjustment to a playback, the adaptation**
55
56 584 **to a real individual, or both, reflect a peculiar vocal behaviour of the individuals we tested and cannot**
57
58 585 **be generalised to the species as a whole. The pups in this study were in a temporarily captive setting,**
59
60 586 **albeit in acoustic proximity to other individuals, similar to conditions they would experience in**
61
62 587 **nature. Unfortunately, vocal development in harbour seal pups has not been studied in wild colonies,**
63
64 588 **hence we do not know whether captivity affects their vocal development. We do know, however, that**
65
66 589 **pups vocally interact with neighbouring pups in the colony and not with their silent mothers; hence**
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68 590

1
2 590 the turn-taking behaviour observed in our captive conditions might extend to the same behaviour in
3
4 591 wild conspecifics.

5 592 Motivation for an individual to respond and engage in an interaction, with the closest partner in
6
7 593 the colony, may depend on the degree of participation signalled by the partner. This, in turn, may be
8
9 594 triggered by individual-specific behaviours or by cues from other modalities. Multimodal
10
11 595 communication should be the target of future studies since we cannot assume that such interactions
12 596 are limited to acoustic cues. Despite these limitations, our study shows that adopting multiple
13
14 597 complementary approaches can be a fruitful way to study rhythmic interactivity in non-human animal
15
16 598 communication.

17 599
18
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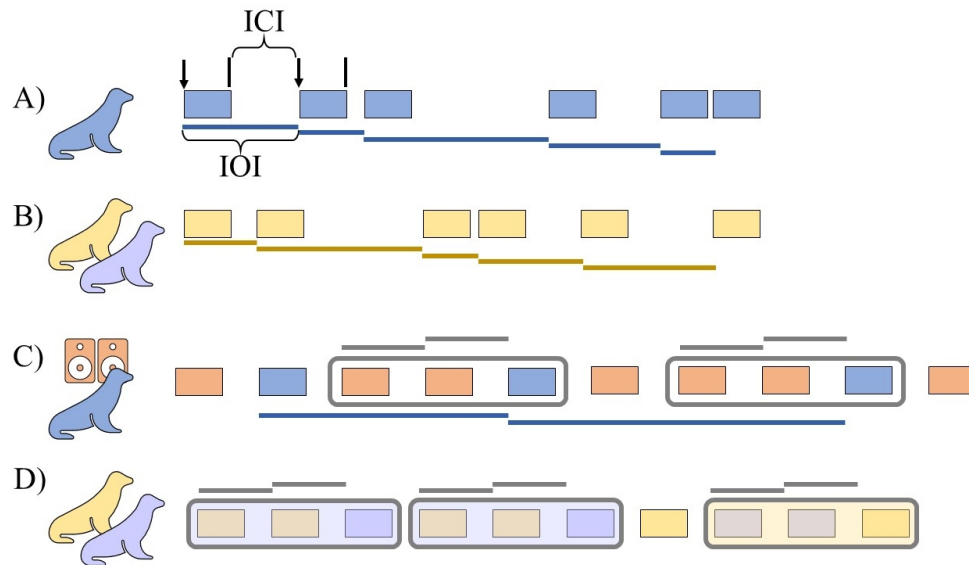


Figure 1. Schematic of experimental conditions and key measurements. Each of the four rows represents one bout and indicates a different behavioural context: (A) alone, (B) silent partner, (C) 1-way interaction, and (D) 2-way interaction. Boxes are coloured to represent the call source and grey rectangles denote vocal interactions. For bouts (C) and (D), calls are isochronously spaced for ease of visualisation, but empirical patterns were not necessarily isochronous. Horizontal bars indicate how IOIs were calculated for different analyses. The call onsets (black arrows) and offsets (black lines) are shown for the first two calls in (A).

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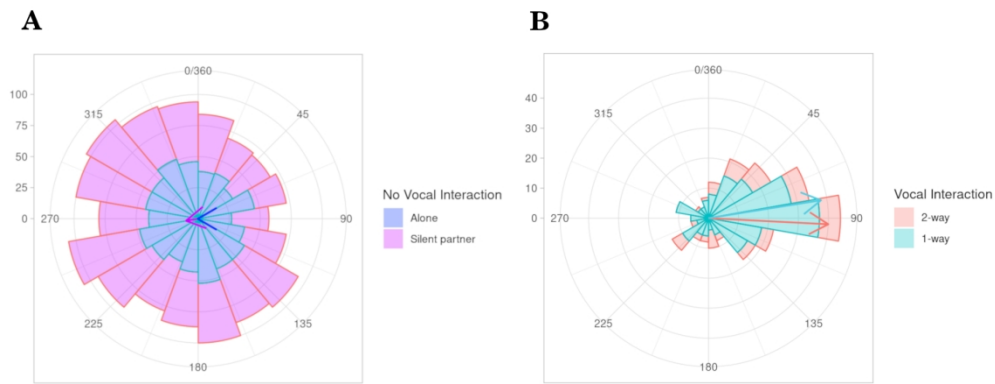


Figure 2. Circular histogram plots (bin width = 20°) showing response phases in (A) both types of behavioural contexts with no vocal interaction (alone/silent partner), and (B) in both types of vocal interaction contexts (1-way/2-way). Angles are measured in degrees starting from 0° and going clockwise to 360°. The arrows indicate the circular mean (μ) and colours correspond to the different behavioural contexts. The length of the arrow corresponds to the value of the mean resultant length (ρ).

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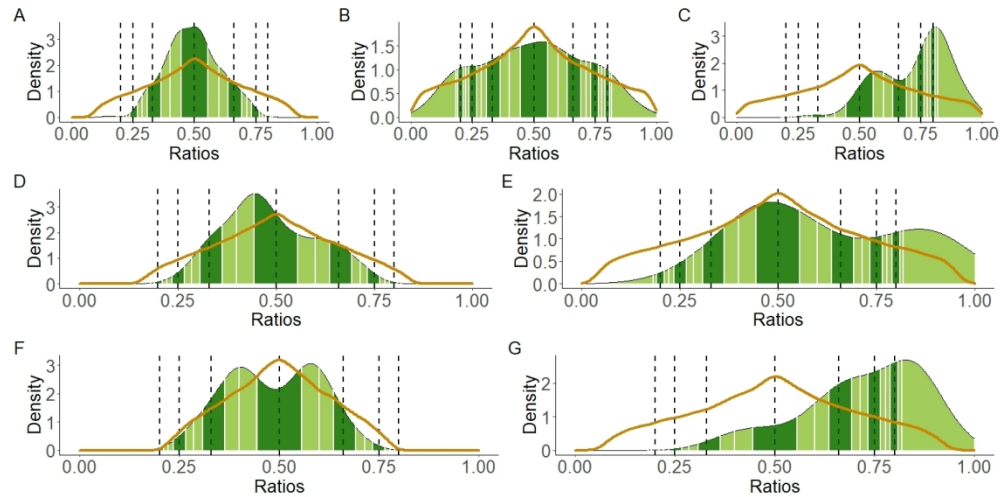


Figure 3. IOI ratio density plots for pups in different behavioural contexts. Pup I: (A) alone, (B) 1-way interaction (disregarding playback), (C) 1-way interaction (responding to playback). Pup A: (D) silent partner, (E) 2-way interaction (responding to partner). Pup B: (F) silent partner, (G) 2-way interaction (responding to partner). For each plot, the dashed vertical lines indicate, from left to right, 1:4, 1:3, 1:2, 1:1 (i.e., isochrony), 2:1, 3:1, and 4:1 small integer ratios. On-integer ratio ranges are in dark green and off-integer ratio ranges are in light green, with white lines and black dashed lines denoting bin boundaries. The orange curves indicate the ratio distribution expected under a uniform distribution if no rhythm categories exist. The empirical ratio distribution significantly differed from the simulated ratio distribution for panels (A), (C), and (G) only. Note that the scale of the y-axes differ.

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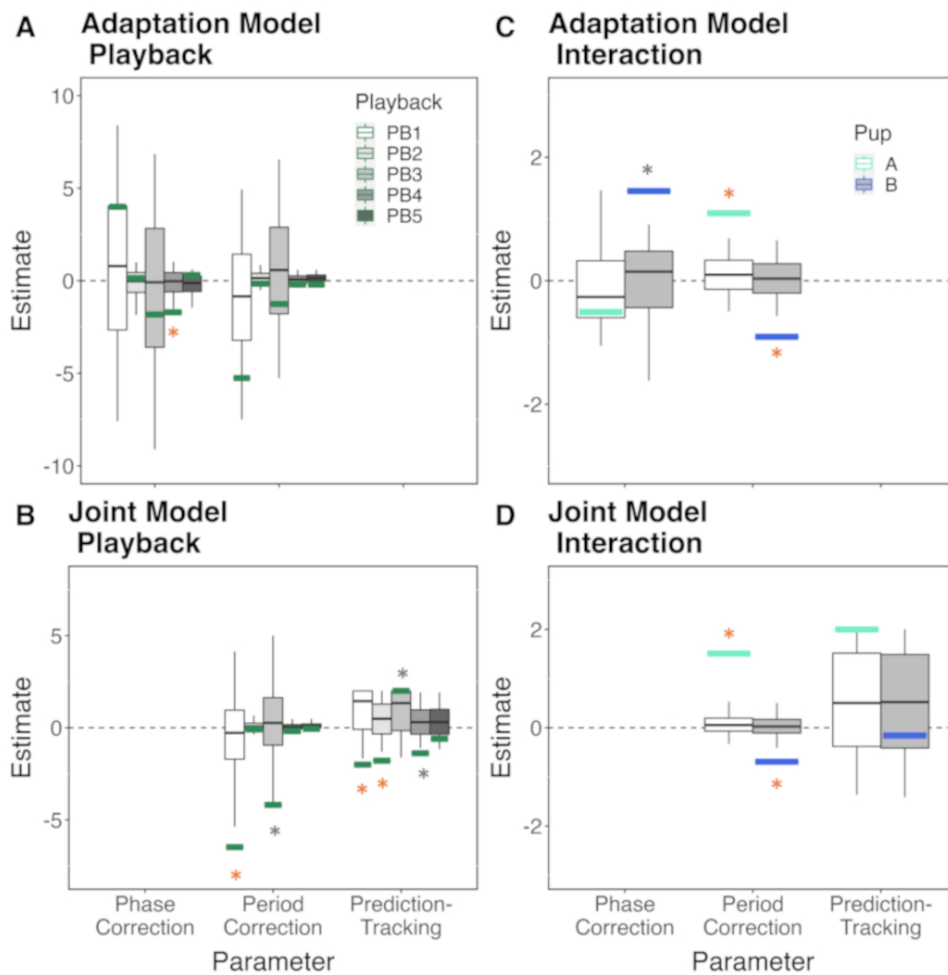


Figure 4. ADAM parameter estimates for seal pups A, B, and I. Left panels (A & B) show parameter estimates for pup I in five playback sessions (1-way interaction); right panels (C & D) show estimates for pups A and B (2-way interaction). Top panels (A & C) show phase correction and period estimates obtained with the adaptation-only version of ADAM; bottom panels (B & D) show period correction and prediction-tracking estimates for the full 'joint' model (anticipatory error correction estimates are not shown). Parameter estimates are shown separately for pup A relative to pup B (aquamarine bars) and pup B relative to pup A (blue bars) in the recording session, and for pup I (green bars) relative to playback calls in separate playback sessions (PB1-PB5). Corresponding parameter estimates for randomly permuted data from each session are represented by box plots, with the central horizontal line indicating the median, the bottom and top edges of the box indicating the 25th and 75th percentiles, and the whiskers indicating the 5th and 95th percentiles. Real estimates with asterisks are significantly different from permuted data estimates at the 2-tailed (orange) or 1-tailed (grey) level.

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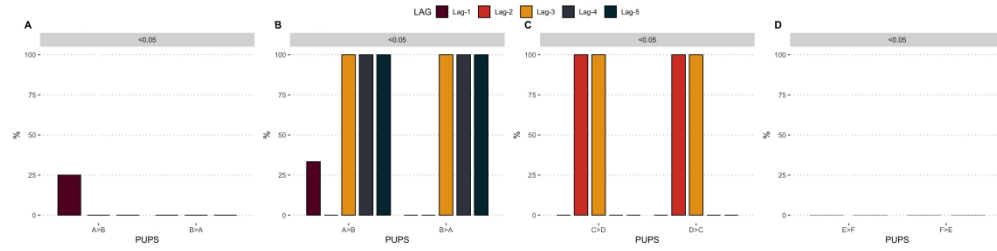


Figure S6. Granger causality results for the 2-way interaction context. The bar plots indicate the percentage of times (y-axis) that the timing of a calling pup was significantly influenced ($p < 0.05$) by another calling pup (i.e., the partner). We considered different pairs of pups bidirectionally and different lag values. We measured Granger Causality for pup pair A/B in two conditions: (A) different bouts within a recording and (B) whole recordings. For pup pairs C/D (C) and E/F (D) we measured Granger Causality only on whole recordings.

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Table 1. Summary table showing in order: research questions, analyses, contributing pups, predictions, whether the data supports each prediction, statistical test(s) used, and result(s) obtained. The column “Supported by data?” has three possible answers: results support the prediction (Y), results only partially support the prediction (Partial), and results do not support the prediction (N). Due to sample size and/or analytical requirements, not all pup data could be used in each analysis. The acoustic variables of interest for the different analytical approaches were: response phases (circular statistics), IOI ratios (categorical rhythms), IOIs (Granger causality, ADAM), and asynchronies (ADAM).

Research question	Analytical approaches	Pups	Prediction	Supported by data?	Statistical test(s) and result(s)
<i>Temporal domain, Q1:</i> <i>Does the presence of a calling partner affect the call timing of individual pups?</i>	Circular statistics	A-I	Pups will not vocalise at random points in time.	Y	Rayleigh test: Unimodal distribution of response phases.
			Pups will call in asynchrony to avoid overlap during vocal interactions.	Y	V-test: Pup calls start at one-quarter of the partner’s period
			Response phases will be affected by the presence of a vocalising partner.	Y	Watson’s U^2 test: Response phase distributions differ between non-interactive and interactive contexts.
	Categorical rhythms	A, B, C, E, H, I	Empirical and chance ratio distributions will only significantly differ when pups are vocally interacting.	Partial	1-sample KS tests: Simulated and empirical ratio distributions are rarely significantly different (exceptions: pup I alone, pup I 1-way, pup B 2-way).
			Vocally interacting pups will have a significant peak at the 4:1 SIR.	N	Paired Wilcoxon signed-rank test: No significant peaks at any of the tested small integer ratios.
			Ratio distributions of individual pups will differ across behavioural contexts.	Y	2-sample KS tests: Ratio distributions significantly differed for the same individuals in different behavioural contexts.

<p>Social domain, Q2: Does the type of calling partner (real or broadcasted) affect the call timing of individual pups?</p>	Circular statistics	A-I	Pups interacting with a real partner will show more adaptive call timing than the pup interacting with a broadcasted partner.	N	Watson's U^2 test: No difference in response phases between 1-way and 2-way interactions.
	Granger causality	A, B, C, D, E, F, I	The time series of a pup will be better predicted considering the time series of a vocalising partner rather than the time series of a broadcasted signal.	Y	Bidirectional & unidirectional causality: Interaction with a real partner impacted the pup's vocal behaviour more than the playback. Mutual temporal adaptation among pairs of vocally interacting pups.
<p>Social domain, Q3: When the focal pup is vocalising, does the presence of a silent partner (vs. no partner) affect call timing?</p>	Circular statistics	A-I	The calling pattern of pups will show similar rhythmic structure in both the alone and silent partner conditions, as no vocal interaction is taking place in both cases.	Y	Watson's U^2 test: No difference between response phase distributions of pup calling alone and pups calling with a silent partner.
<p>Cognitive domain, Q4: Which timing mechanisms are used by pups during vocal interactions?</p>	ADAM	A, B, I	In the 1-way interaction, pups may show sensitivity to (non-)interactivity which would be reflected by parameter changes over repeated sessions. The 2-way interaction may be mediated by basic temporal adaptation and possibly higher-level anticipatory timing.	Partial	1-way interaction: Temporal anticipation, and to a lesser extent also adaptation, decreased across the playback sessions, and was absent in the final session. 2-way interaction: Clear evidence for temporal adaptation, with differing parameter estimates for each seal pup suggesting the emergence of different interactive roles.