

18 recent research showed some evidence of cooperative turn-taking also in other animal species.
19 However, systematic evaluations and comparisons of turn-taking skills within and across species
20 pose considerable challenges due to different measures applied and research foci on specific
21 elements. Here, we build on a comparative framework resting on four key elements of human
22 conversational turn-taking - flexibility, participation frameworks, temporal relationships, and
23 adjacency pair-like sequences - to enable standardized and feasible annotation procedures across
24 species and taxa. Proposed parameters are described in detail, and their operationalization is
25 outlined through step-by-step annotation schemes and real-world examples. By understanding
26 which elements of turn-taking are shared across different model systems and taxa and by mapping
27 similarities and differences, this standardized “turn-taking toolkit” will aid in fostering a more
28 biocentric perspective on the evolution of communication and gaining a better understanding of
29 the evolutionary origins of language and cooperation.

30

31 **Keywords:** social interaction; research methods; language evolution; communication; cooperation

32 **1. Introduction**

33 One of the most distinctive features of human cooperation is its complexity compared to
34 other species, enabling individuals to engage in highly structured social interactions (e.g., Apicella
35 & Silk, 2019; Burkart et al., 2009; Melis & Semmann, 2010). These interactions are frequently
36 accompanied by conversational turn-taking (hereafter turn-taking) - classically used to describe
37 the alternating production of vocalizations using a variety of linguistic and non-linguistic cues
38 between two or more individuals (Holler et al., 2015; Sacks et al., 1974). This fundamental
39 mechanism has been suggested to be the foundation of most human interactions that regulates
40 exchanges and facilitates coordination between interactants’ mutual understanding (Levinson,
41 2006). Moreover, it has been suggested to be governed by universal properties that regulate turn
42 allocation (whose turn it will be), turn transitions (when the next turn can be made and how to
43 avoid overlap), turn size (duration of a specific turn; Clark, 1996; Sacks et al., 1974), and turn
44 content (sequence organization; e.g., Schegloff, 2007). Beyond its structural role, turn-taking is
45 highly cognitively demanding with human response times during conversation averaging between
46 0-500ms, matching the duration of an eyeblink (Stivers et al., 2009). This fast timing suggests that

47 interactants listen to and process the acoustic information while simultaneously planning a
48 response (Levinson & Torreira, 2015).

49 At the beginning of the 21st century, Levinson (2006) proposed that turn-taking is part of
50 a package of underlying propensities in human communication, including face-to-face interactions
51 that afford the use of gesture and gaze, and the motivation and interest in other minds, termed the
52 *interaction engine*. Turn-taking may represent the most ancient mechanisms of the layered system
53 of language and thus may have predated language. Support for this hypothesis stems from infant
54 studies showing that cooperative turn-taking skills precede gestural and linguistic competence (so-
55 called “proto conversations”), and play a key role in language development (e.g., Bruner, 1975;
56 Clark, 2009; Ginsburg & Kilbourne, 1988), studies suggesting universality of turn-taking across
57 cultures and languages (e.g., Stivers et al., 2009) as well as evolutionary precursors across different
58 clades of primates (e.g., Levinson, 2016), raised the question of its biological bases and
59 evolutionary trajectory. Recently, comparative researchers thus started to test whether turn-taking
60 may be the evolutionary “missing link” bridging linguistic and non-linguistic species (e.g.,
61 meerkats (*Suricata suricatta*): Demartsev et al., 2018; starlings (*Sturnus vulgaris*): Henry et al.,
62 2016; African elephants (*Loxodonta africana*): O'Connell-Rodwell et al., 2012; marmosets
63 (*Callithrix jacchus*): Takahashi et al., 2013). (For overviews of other phenomena such as
64 antiphonal calling, duetting and chorusing, please also see Ravignani and colleagues (2019) and
65 Vanderhoff and Hoverud (2022)). To date, studies across insects, anurans, birds, and mammals
66 revealed features reminiscent of human turn-taking - such as the existence of distinct time
67 windows, adjacency pair-like sequences, overlap avoidance, and cues for turn allocation (for
68 reviews, see: Abreu & Pika, 2022; Pika et al., 2018; Pognault et al., 2020; van Boekholt et al.,
69 2025).

70 Despite the findings, meaningful comparisons of evolutionary precursors of human turn-
71 taking elements and shared features have been constrained by variation across employed
72 definitions, methodologies and applied measures (Pika et al., 2018). Specifically, studies currently
73 face three major constraints: (i) the lack of uniformity concerning the use of terms and criteria of
74 turn-taking across and within scientific fields hampering valid cross-species comparisons (Abreu
75 & Pika, 2022; Pika et al., 2018); (ii) the limited number of studies investigating the hallmarks of
76 human turn-taking, which have been biased toward single elements (e.g., temporal relationships)

77 and modalities (e.g., vocal exchanges). Since communication is inherently multimodal (e.g., Holler
78 & Levinson, 2019; McNeill, 1992) these biases have hampered a comprehensive understanding of
79 existing turn-taking systems, its evolutionary trajectory, and systematic, quantitative, and direct
80 comparisons with human conversational turn-taking; (iii) the existing research bias toward
81 nonhuman primates, limiting our understanding of whether turn-taking is a species-specific
82 adaptation to social or environmental requirements or whether turn-taking is a phylogenetically
83 conserved trait maintained across lineages through common descent (e.g., Ord et al., 2021).
84 Consequently, the disparate use of definitions and measures has made direct, quantitative
85 comparisons between human and non-human turn-taking systems exceptionally difficult,
86 necessitating a more standardized and inclusive methodological approach.

87 To tackle these issues and foster systematic comparisons, Pika and colleagues (2018)
88 pinpointed the four most crucial hallmarks of human conversational turn-taking (Sacks et al., 1974)
89 and designed a comparative framework. It addresses:

90 1) *Flexibility of turn-taking organization* (how is it organized?) This element concentrates
91 on the variety of size and ordering turns and the ability to adjust signals and actions (see Table 1
92 for definitions) in an interaction in case of a lack of a response.

93 2) *Participation framework* (who is taking the next turn?). This element focuses on the
94 initiation of turns (who can or should produce the next signal) and techniques for attributing the
95 next turn as the interaction is ongoing.

96 3) *Temporal relationships* (when do response turns occur?). This element addresses the
97 time window between two turns during an interaction.

98 4) *Adjacency pair-like sequences* (what should the next turn do?). This element consists of
99 a minimum of two turns by different participants, where a first pair part (e.g., requests) is followed
100 by a predictable response in the form of a second pair part (e.g., grants).

101 Despite their aim of translating human linguistic complexity into applicable universal
102 behavioral parameters, the field still lacks a standardized and easy-to-use method for annotation
103 and comparing all four elements simultaneously. Most studies continue to rely on different metrics
104 or focus on single elements, limiting robust cross-species comparisons and limiting our

105 understanding of the evolutionary roots of coordinated interactions (but see van Boekholt et al.,
106 2025 for an overview).

107 Therefore, we present a refined, operationalized toolkit for investigating the underlying
108 elements of turn-taking across the animal kingdom and provide a revised, expanded definition of
109 turn-taking compared to Pika and colleagues' (2018). It now refers to “the orderly exchange of
110 communicative signals and/or behaviors between at least two individuals, governed by
111 coordination principles that regulate turn transfer”. The coordination of turn transfer should follow
112 species-specific principles that vary in form (flexibility), sequence (contextual fit, adjacency pair-
113 like structures), duration (temporal relationships), and distribution (turn allocation). In animals,
114 turn-taking systems can involve various forms of exchanges, such as action-action (e.g., A grooms
115 B, B grooms A), action-signal (e.g., A grooms B, B PRESENTS to A), signal-action (e.g., A
116 PRESENTS to B, B grooms A), or signal-signal (e.g., A PRESENTS to B, B PRESENTS to A)
117 interactions. While this is most often not researched in human studies (for exceptions, please see
118 Drew & Couper-Kuhlen, 2014; Drew & Kendrick, 2018), our framework explicitly incorporates
119 behavioral social actions alongside signals.

120 Unlike traditional methods that focused almost exclusively on acoustic exchanges (e.g.,
121 antiphonal calling), our approach recognizes that turn-taking can manifest as signal-signal, action-
122 action, or mixed-modality interactions (e.g., a gesture followed by a vocalization, or reciprocal
123 grooming; Kolff & Pika, 2025; Tibesar et al., 2026; van Boekholt & Pika, 2025). By defining turn-
124 taking through coordination principles rather than specific modalities, this toolkit allows for the
125 systematic annotation of all types of social exchanges, such as play, grooming, food sharing,
126 mating, and other cooperative exchanges, under the same analytical lens as conversation.

127 Beyond moving from current theoretical frameworks to a universal toolkit, our aim was
128 threefold. First, while previous studies investigated predominantly single elements (e.g., temporal
129 relationships), here we introduce robust and feasible metrics for capturing the complete spectrum
130 of turn-taking. Secondly, we demonstrate how these measures can be reliably applied across
131 various communicative modalities as well as across taxa. Third, unlike theoretical frameworks or
132 empirical research, we provide a detailed annotation guide with step-by-step processes and real-
133 life examples to facilitate usage and implementation by other researchers.

134 Crucially, this toolkit is presented here as a methodological instrument for empirical testing
135 rather than a claim of universal presence. Our goal is to provide the necessary metrics to distinguish
136 between random behavioral successions and structured, coordinated turn-taking exchanges,
137 acknowledging that not all animals may exhibit the same elements or degree of turn-taking. By
138 assessing each component of turn-taking independently, the toolkit allows researchers to build a
139 detailed profile for each species - identifying which elements are present, which are absent, and to
140 what extent the overall pattern resembles human turn-taking. This approach facilitates systematic
141 cross-species comparisons, enabling researchers to identify both the specific features that bring a
142 species' communication system closer to or further from human-like turn-taking, and the
143 ecological, cognitive, or social factors that may drive these similarities and differences. In
144 particular, this enables researchers to identify both shared evolutionary origins (homologies)
145 among closely related species (e.g., great apes) and functional similarities (analogies) in distantly
146 related species (e.g., cetaceans). Thus, by establishing a standardized and comprehensive
147 framework for turn-taking, this work provides a crucial foundation for advancing comparative
148 research on communication systems, paving the way for deeper insights into the adaptive processes
149 and selective pressures that shape this fundamental communicative behavior.

150

151 **2. Methods: Description and implementation**

152 **2.1. Annotation Scheme**

153 Among the plethora of in-video behavioral annotation programs (e.g, Boris, Observer), we
154 suggest using ELAN (<https://archive.mpi.nl/tla/>) for several reasons. Most importantly, ELAN is
155 the predominant tool in human language and communication research, making our cross-species
156 coding scheme directly comparable to and compatible with existing human interaction corpora. Its
157 hierarchical tier system is also particularly well-suited to the complexity of multimodal data,
158 allowing researchers to map overlapping behavioral information, such as vocalizations, gaze, and
159 social actions, onto a synchronized timeline with exceptional timestamp precision. This is critical
160 for capturing the fine-grained temporal dynamics of turn-taking and communicative exchanges.

161 Moreover, we introduce a custom annotation scheme, designed to enable standardized
162 cross-species turn-taking analysis. While the custom annotation scheme was built within ELAN
163 and takes full advantage of its hierarchical tier system - features that are not always available or

164 equivalently implemented in other platforms -, the underlying coding logic and term definitions
165 are in principle transferable to alternative programs with some adaptation effort. Researchers
166 choosing to do so should be aware that certain structural elements may need to be simplified or
167 reorganized to fit the constraints of their preferred software, and we do not provide ready-made
168 templates for those environments. For ELAN users, we have made the template files and annotated
169 real-life examples in ELAN available on Figshare (<https://figshare.com/s/c9fe94c30ebad0ed9c7d>)
170 to facilitate immediate implementation. A comprehensive description of the coding process and
171 definitions of all tiers and terms is provided in Section 2.

172 Additionally, although a full tutorial on ELAN is beyond the scope of this study,
173 researchers can find detailed protocols for its application in behavioral coding elsewhere
174 (<https://greatapesgestures.github.io/download/>; <https://tinyurl.com/yvdcdpzn>; Genty & Fuchs,
175 2023; Grund et al., 2024 supplementary work). To investigate the four elements of turn-taking,
176 audio and video data can be used, with synchronization of both being the preferred option for
177 multimodality purposes.

178 Before coding, we recommend the development of a standardized ethogram (Altmann,
179 1974) to define the behavioral repertoire of the target species. While the specific content of an
180 ethogram will naturally differ across taxa, the functional classification of the behaviors should
181 remain consistent to ensure cross-species comparisons. Specifically, researchers must clearly
182 distinguish between gestures (communicative signals) and social actions (mechanical behaviors).
183 Otherwise, comparisons may be biased (e.g., one may find that species A uses more social actions
184 than species B, but while looking more into the comparing ethograms, the social action for species
185 A was a gesture for species B; Genty et al., 2009; Pika, 2008). Furthermore, certain behaviors may
186 transition between these categories depending on the context and physical execution (e.g., push
187 and pull). For example, if a chimpanzee gently pushes another chimpanzee's arm to groom this, it
188 would be annotated as a gesture, whereas if the chimpanzee pushes the other chimpanzee so that
189 the other falls on the ground because of the force exerted, this would be annotated as an action. To
190 address these complexities, please see Table 1 for our definition of communicative modalities and
191 the fulfillment of primary criteria and Table S1 for how to annotate them.

192 Table 1. Definitions of different terms used in a turn-taking interaction.

Terms	Definition
<i>Signals</i>	Production of information via a stimulus (e.g., facial expressions and gestures, and vocalizations; Marler, 1967).
<i>Facial Expressions</i>	Expressive movements of different facial muscles, such as mouth, cheeks, lips, or eyes, to produce a visual signal (Liebal et al., 2004).
<i>Gestures</i>	Movements of the extremities or head and body postures that are directed to a social partner, mechanically ineffective – meaning produced to request or reach a goal, requiring active participation of the interactant - and potentially elicit a response by the recipient (Grund et al., 2024; Pika, 2008).
<i>Vocalizations</i>	Sounds produced via the vibration of vocal folds of the larynx voluntarily or involuntarily (Nieder & Mooney, 2020).
<i>Oro-facial sounds</i>	Sounds produced with the lips and/or teeth (mouth can be opened or not), without passing air via the vocal folds.
<i>Multi-modal signals</i>	Fixed multi-modal signals, such as the “scream face” in chimpanzees that is always coupled with a “scream vocalization” due to production mechanics, involve obligatorily linked modalities, and free multi-modal signals, like the “pout face” that may or may not be accompanied by a vocalization, are flexibly combined and not biomechanically constrained (Partan & Marler, 2005).
<i>Social Actions</i>	Any socially directed embodied behavior that leads to the perceived goal through direct manipulation of another’s body/body parts or the movement of one’s own body (Fröhlich et al., 2016).
<i>Interactions</i>	Alternation of produced social actions and verbal and/or non-verbal signals between participants that co-inhabit a shared environment (Enfield & Levinson, 2006).
<i>Turns</i>	Signals or actions made by one individual to initiate, continue or end an interaction.

193

194 **2.2. Inter-Rater reliability**

195 To ensure consistent application of the coding scheme, we recommend conducting inter-
196 rater reliability assessments. Individuals blind to the hypotheses should independently annotate a

197 randomly selected subset (e.g., 15%) of the data, and agreement should be assessed using a statistic
198 appropriate for the type of data (e.g., Cohen’s Kappa for categorical data, or EasyDIAG in ELAN
199 itself; Holle & Rein, 2015). An acceptable threshold for agreement should be established a priori
200 (e.g., Kappa > 0.70), and discrepancies should be resolved through discussion and consensus, and
201 coding guidelines should be refined as needed.

202

203 **2.3. Turn-taking elements: Metrics applied and how to annotate them**

204 Note: All coding examples shown are hypothetical demonstrations. Specific rules (e.g., response
205 timing) should be established based on species-specific data.

206

207 *A. Flexibility of turn-taking organization*

208 *Question:* How is the interaction organized? This element refers to the variety of size and ordering
209 of turns, markers of goal-directed behavior, and the ability to adjust, combine and/or change
210 signals/actions in an interaction to achieve the desired goal (Abreu & Pika, 2022; Pika et al., 2018;
211 Fig. 1&2).

212 *Operationalized parameters:* Flexibility can be assessed by quantifying response waiting,
213 repetition (persistence and elaboration), and turn transitions utilizing the following tiers (Table
214 S1): Vocalizations, Gestures, Facial Expressions, Actions, and Repetition. Repetition is annotated
215 in real-time as observed, while response waiting and turn transitions are identified during the
216 analysis phase.

217 (a) Response waiting - period during which an initiator pauses after producing a
218 signal/action, anticipating a response from the recipient. The waiting period should last
219 at least 1 second (Hobaiter et al., 2017) depending on the species. If no response is
220 received within this time, the interaction can be annotated as “No Response”.

221 (b) Repetition (e.g., Fröhlich & van Schaik, 2022; Roberts et al., 2013) - situations where
222 an individual reiterates a signal/action after a pause (see definition in participation
223 framework element) until a response is received (species-specific timing). Repetition
224 can be categorized as:

- 225 a. Persistence: The exact same signal/action is repeated after a pause (see Fig. 1);
226 b. Elaboration: Another signal/action is repeated after a pause (see Fig. 2)¹.

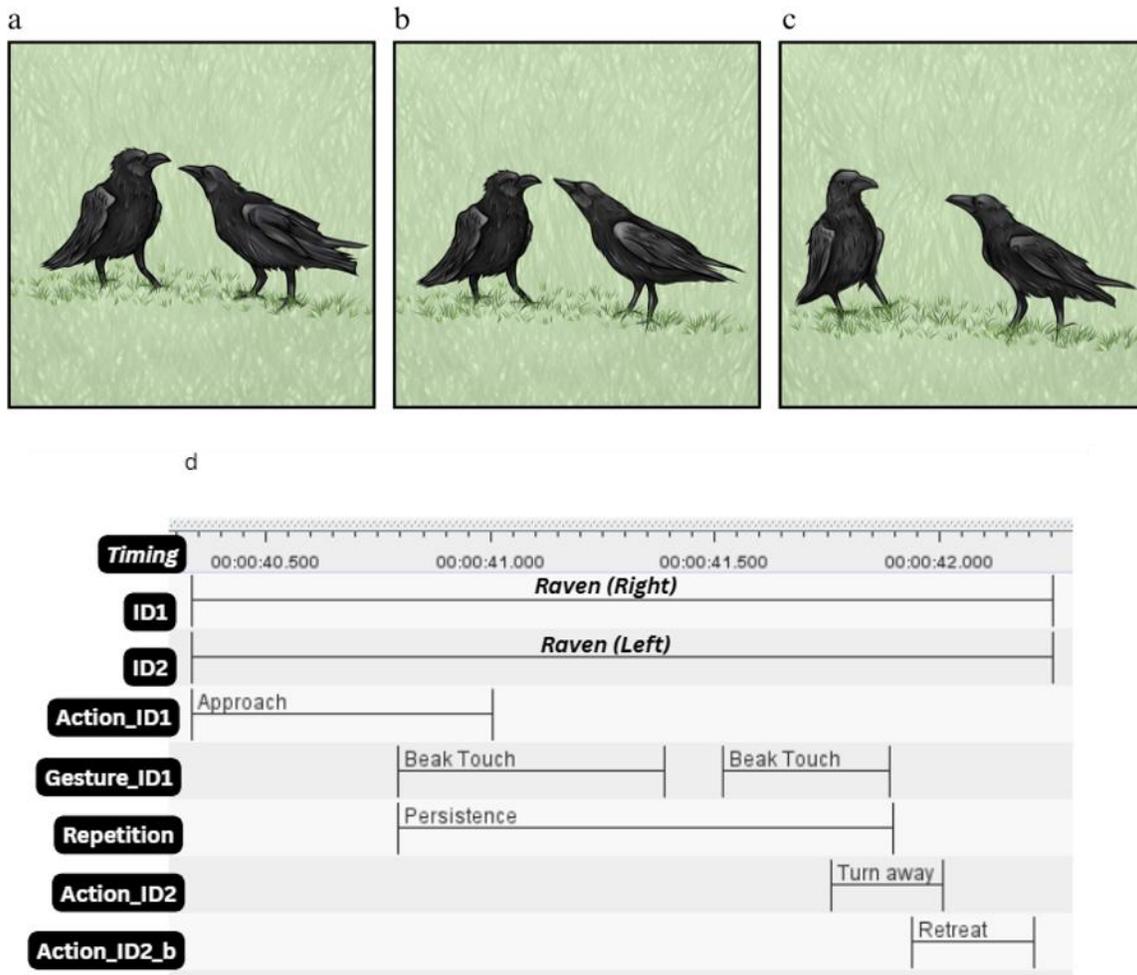
227

- 228 (c) Turn transitions - identified by consecutive signal/action pairs produced by different
229 individuals within an interaction. These transitions should be visible upon completion
230 of the coding process (see adjacency pair-like sequences for further information).

231 *Coding Considerations:* Ambiguous responses should be discussed in detail with other annotators
232 to determine whether it constitutes a valid response. Additionally, species-specific maximum
233 waiting times should be determined, with particular consideration of whether the individual is
234 monitoring (gaze and body orientation) the partner.

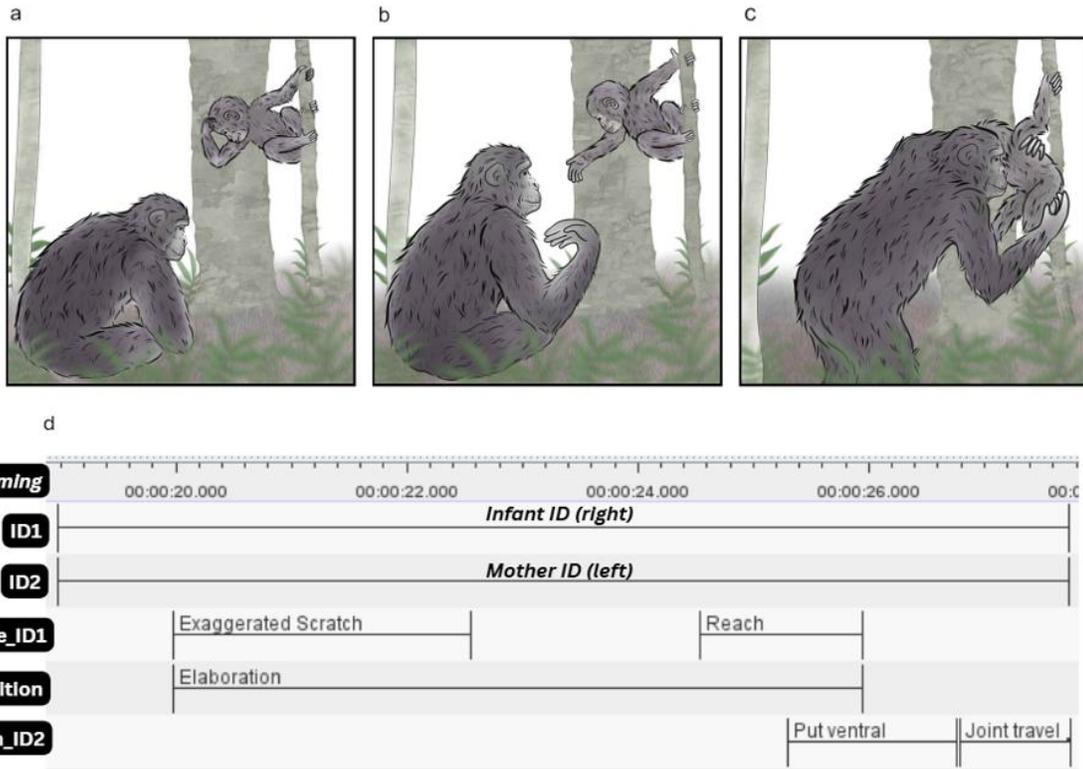
235 With these three distinct metrics, we can quantify the frequency of actions, gestures, vocalizations,
236 facial expressions, and multifaceted combinations (any multimodal and multicomponent
237 combinations of the above-mentioned tiers from the same individual; see Fröhlich & van Schaik,
238 2018; Hex & Rubenstein, 2024 for details on multimodality and multicomponent communication)
239 during a turn-taking event. Further analysis can also explore the variation of sequences exchanged
240 between initiator and recipient, and their respective participation roles within and over multiple
241 interactions - for example, identifying recurring patterns such as A-B-A or A-B-C (but see Fröhlich
242 et al., 2025 for a thorough review on flexibility). Notably, response waiting and
243 persistence/elaboration may indicate attempts at repair - “fixing” a misunderstanding or
244 communicative breakdown (Schegloff, 2007) - in situations where an adequate response is not
245 immediately received (e.g., Heesen et al., 2022).

¹ There may be exceptions to these outlined cases, but see temporal relationships for further information.



246

247 *Figure 1.* Flexibility element in an interaction between two ravens (*Corvus corax*): (a) ID1 approaches and
 248 tries to TOUCH ID2 with his beak; (b) when ID2 does not respond (~0.2s), ID1 repeats the gesture
 249 (persistence) while also coming closer; (c) ID2 turns her body away and retreats; (d) ELAN screenshot of
 250 the annotated interaction using the tiers from Table S1. © Luara Martins.



251

252 *Figure 2.* Flexibility element in the joint travel context in a chimpanzee (*Pan troglodytes*) mother (ID2) and
 253 her infant (ID1): (a) ID1 performs an EXAGGERATED LOUD SCRATCH toward her mother and waits; (b) after
 254 ~2s, ID1 produces a REACH (elaboration); (c) ID2 responds by positioning her infant ventral for travel; (d)
 255 ELAN screenshot of the annotated interaction using the tiers from Table S1. © Luara Martins.

256

257 *B. Participation framework*

258 *Question:* Who is taking the next turn? This element focuses on the initiation of turns (who can or
 259 should produce the next signal), and the capacity and/or techniques used for attributing the next
 260 turn to another individual/audience (Pika et al., 2018; Fig. 3&4).

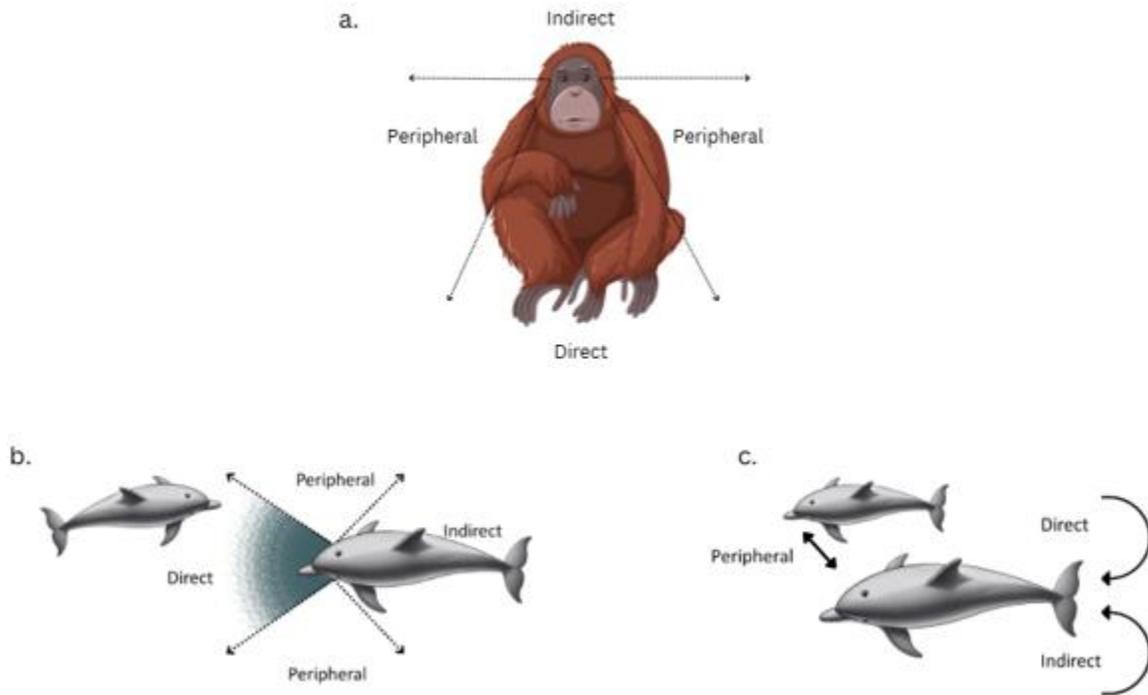
261 *Operationalized parameters:* Participation framework can be assessed by quantifying orientation
 262 patterns, proximity dynamics, pauses, and phase responses utilizing the following tiers (Table S1):
 263 Gaze, BodyOrientation, and Proximity. Orientation and Proximity are annotated in real-time as
 264 observed, while pauses and phase responses are identified after coding.

- 265 (a) Orientation (Fig. 3) - directional alignment of interacting individuals, encompassing
266 both attentional state and bodily direction. Orientation can be categorized as either
267 Gaze- or Body-directed:
- 268 a. Gaze: Face direction is defined as the angle between the initiator's face and the
269 body position of the other individual. Whenever possible, focusing on the eye
270 gaze of the initiator is preferable, as this gives finer details.
 - 271 b. Body: Shoulder and chest direction (species dependent) can be used as metrics,
272 and defined as the angle of these areas of the initiator in relation to the other
273 individual.
- 274 (b) Proximity - spatial distance maintained between interacting individuals throughout the
275 interaction sequence. We recommend coding it by using categories based on the
276 anatomy of the respective model species and the type of data collected:
- 277 a. Video data: Using species-specific body measurements (e.g., arm's length, body
278 length) rather than absolute metric distances (e.g., meters) may provide more
279 reliable proximity criteria across different taxa.
 - 280 b. Audio data: Distinguish between visible and not visible proximity at the
281 beginning of an interaction during data collection.
- 282 (c) Pauses - time elapsed (offset-onset) between two consecutive signals/actions produced
283 by the same individual when there is no response from another individual.
- 284 (d) Phase responses — time elapsed (offset-onset) between two separate signals/actions
285 produced by the same individual with another individual producing a signal/action in
286 between. We recommend comparing pauses, phase responses, and response latencies
287 (see temporal relationships) to allow the assessment of how an individual's signaling
288 timing is influenced or adjusted by others. This comparison helps identify the
289 mechanisms by which turns are allocated and coordinated during an interaction.

290

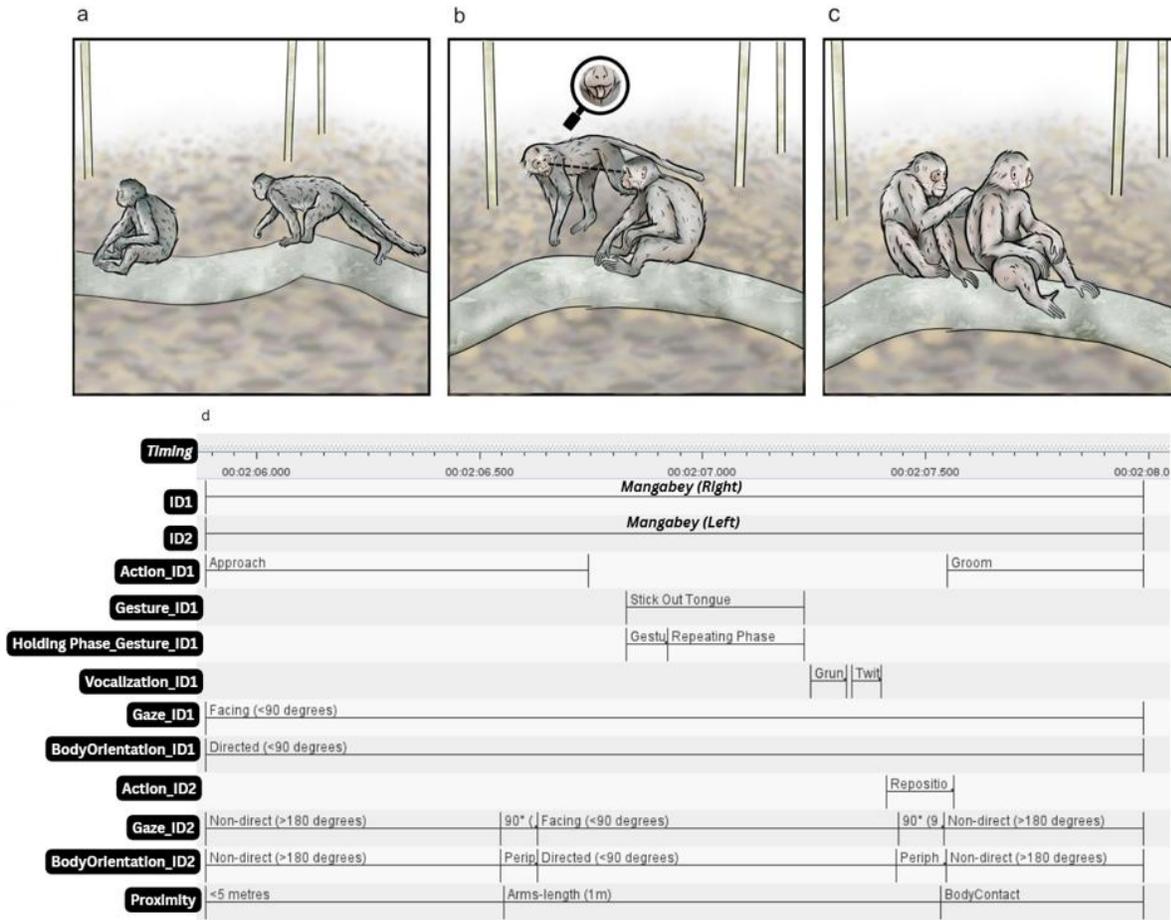
291 *Coding Considerations:* We recommend adapting the degrees of orientation to the study species
292 and to annotate orientation within a cone shape, so that individuals are considered facing even if
293 their gaze is directed slightly upward or downward (Fig. 3). Orientation coding applies solely to
294 video footage and is continuously annotated from the onset (or earlier for a more detailed

295 depiction) of an interaction until one (or both) of the interactors end the interaction, or until
 296 individuals are no longer visible. Due to the inherent constraints of animal movement, angular
 297 transitions cannot skip intermediate ranges (e.g., moving from $<90^\circ$ to $>180^\circ$ must include coding
 298 for 90° - 180°). For audio-only data, pauses and phase responses can serve as the primary metric for
 299 assessing participation framework when orientation cannot be determined.



300

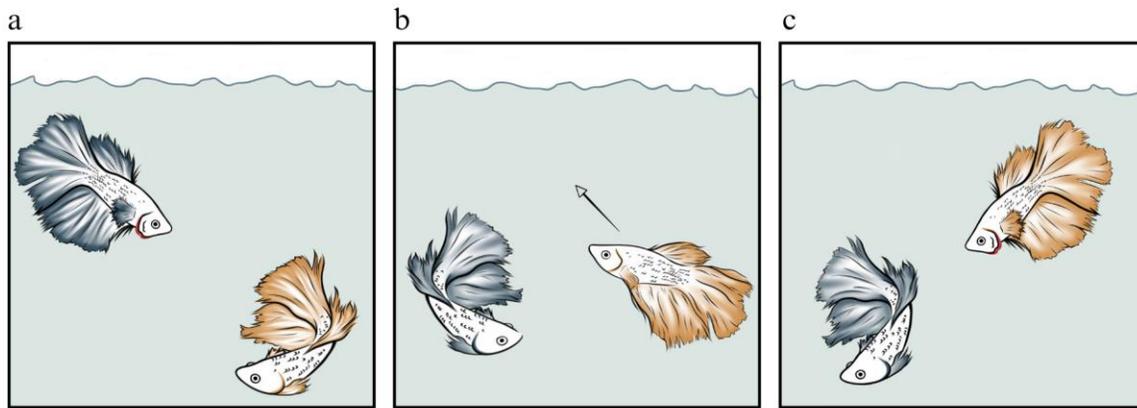
301 *Figure 3.* Illustration representing gaze direction and body orientation categories: (a) animals with front-
 302 facing eyes: $<90^\circ$ (Direct), 90° - 180° (Peripheral), $>180^\circ$ (Indirect) (e.g., Pika et al., 2003); b. gaze direction
 303 animals with lateral-facing eyes: $<60^\circ$ (Direct), 60 - 200° (Peripheral), $>200^\circ$ (Indirect) (e.g., Connor &
 304 Smolker, 1996); and (c) body orientation for lateral-facing eyes relative to conspecific. In the illustrated
 305 position, the orientation is peripheral; if the individual rotates so that its belly faces the other, the orientation
 306 is direct, whereas turning the back toward the other indicates indirect orientation.



307

308 *Figure 4.* Participation framework element in a grooming initiation in sooty mangabeys (*Cercocebus atys*):
 309 (a) ID1 approaches within <5m (Proximity), gazes at ID2 (<90°) who does not look at ID1 (gaze direction:
 310 >180°); (b) in arm's length to ID2, ID1 directs her gaze (<90°), performs TONGUE OUT, and produces a
 311 GRUNT and a TWITTER; ID2 matches gaze and body orientation (<90°); (c) ID1 begins grooming after 0.2s;
 312 (d) ELAN screenshot of the annotated interaction using the tiers from Table S1. © Luara Martins.

313



d



314 *Figure 5.* Participation framework element in agonistic visual displays of Siamese fighting fish (*Betta*
 315 *splendens*) (based on the study of Everett et al., 2025): (a) ID1 (blue fish) elevates in the water column and
 316 produces FLARE while facing forward; (b) as ID1 turns laterally, ID2 (orange fish) elevates and orients
 317 toward ID1; (c) ID2 produces FLARE while elevated and facing forward as ID1 turns away and descends in
 318 the water tank; (d) ELAN screenshot of the annotated interaction using the tiers from Table S1. © Luara
 319 Martins.

320

321 *C. Temporal relationships*

322 *Question:* When do response turns occur? This element addresses the time window between the
 323 signal/action, and its response, which can be species (Pika et al., 2018) and possibly also modality
 324 and context-specific (Fig.7).

325 *Operationalized parameters:* The temporal relationship has been the most investigated element
326 (e.g., Pournault et al., 2020; Ravnani et al., 2019; van Boekholt et al., 2025), and can be analyzed
327 by quantifying response latency patterns, gap and overlap distributions, and timing variations by
328 calculating timing differences between relevant tiers (Table S1). All temporal measurements are
329 derived during the analysis phase by measuring time differences between annotated signals/actions
330 across different individuals. Rather than selecting a metric arbitrarily, the choice should be guided
331 by the research question under investigation.

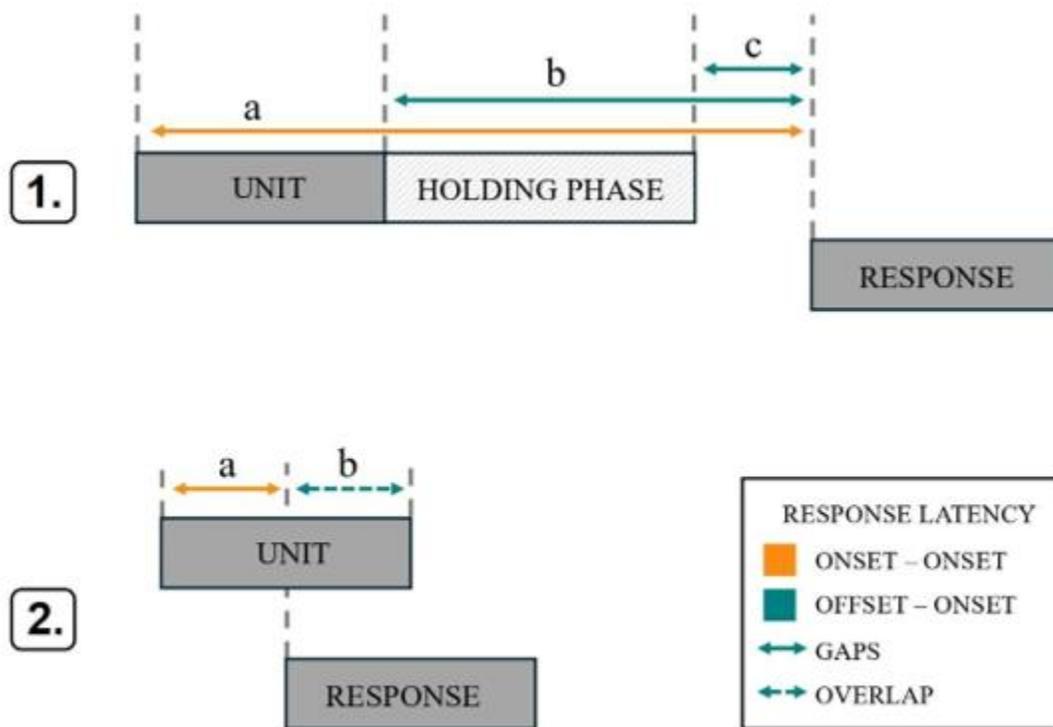
332 (a) Response Latency - time elapsed between two consecutive signals/actions, or signal-action
333 combinations produced by the different individuals involved, encompassing gaps and
334 overlaps in turn transitions (this is, between turns; Fig. 6). Response latency can be
335 categorized based on measurement approach:

336 a. Onset-to-Onset: Measures the time an individual takes to “understand” a signal or
337 action - recommended when the focus is on how promptly an individual responds
338 in relation to the start of articulation (e.g., in humans, this would involve the
339 cognitive processes that occur before a signal/action is fully articulated), but does
340 not include overlap avoidance. This is analogous to measures used in human sign
341 language research (e.g., De Vos et al., 2016), making it particularly suitable for
342 comparisons involving species with prominent gestural communication (e.g.,
343 primates).

344 b. Offset-to-Onset: Measures the time between the end of one signal/action and the
345 start of the next - recommended when the focus is to examine the capacity of the
346 animal to avoid overlap and respond promptly or for interactions that are mainly
347 vocal. This is analogous to measures used in human vocal language research (e.g.,
348 Stivers et al., 2009), making it particularly suitable for comparisons involving
349 species with prominent vocal communication (e.g., birds).

350 c. Holding Phase: Measures the time from the moment the signal/action has been fully
351 executed until the position is fully retracted (e.g., the RAISE ARM gesture in
352 bonobos) or has received a response (e.g., the PRESENT gesture in chimpanzees for
353 grooming purposes).

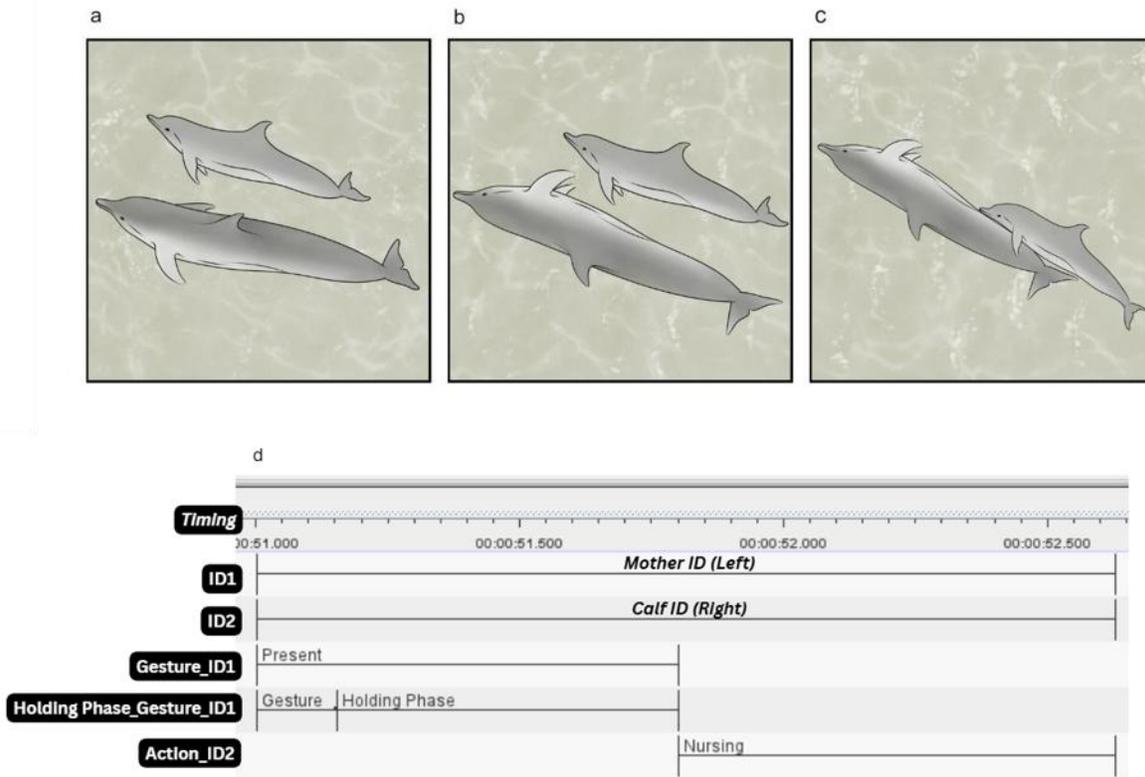
354 *Coding Considerations:* To ensure robust cross-species comparisons, researchers must adopt a
 355 consistent temporal anchor for measuring turn transitions. We have provided three standardized
 356 metrics (onset-to-onset, offset-to-onset, or holding-to-onset) to accommodate the diverse physical
 357 properties of different communicative modalities. Thus, the choice should align with the respective
 358 research objectives and the specific cognitive or behavioral processes under investigation, as well
 359 as the modalities examined. While all of the aforementioned metrics are valid, it is crucial to
 360 specify and report which metric was employed in the methods section of the resulting manuscript
 361 to allow for proper comparisons. Species-specific timing constraints should be established based
 362 on modal characteristics and ecological context. Finally, to investigate sequences of
 363 signals/actions, we suggest using the offset of the last signal/action of the sequence to the onset of
 364 the response because this method allows for an analysis of the continuity and flow of interactions,
 365 helping to understand how individuals manage the timing of their responses within a sequence.



366

367 *Figure 6.* Diagram representing different operational ways of annotating a response latency within an
 368 interaction for a 1. non-overlapping response or 2. overlapping response: (a) unit (signal/action) onset to

369 response onset (the individual may respond before the signal/action is complete); (b) unit (signal/action)
 370 offset (for gestures, it is the end of fully executed gesture) to response onset encompassing gaps and
 371 overlaps; and (c) gesture holding phase offset (retraction point) to response onset. Note that this can be used
 372 for multiple modalities.



373
 374 *Figure 7.* Temporal Relationships element in the nursing context of dolphins (*Tursiops spp.*): (a) mother
 375 (ID1) and calf (ID2) swim side by side in close proximity; (b) ID1 PRESENTS her belly to ID2; (c) ID2
 376 begins nursing with a latency of 0.8s (onset-onset), 0s (offset-onset including holding phase), or 0.65s
 377 (offset-onset excluding holding phase); (d) ELAN screenshot of the annotated interaction using the tiers
 378 from Table S1. © Luara Martins.

379

380 *D. Adjacency pair-like sequences*

381 *Question:* What should the next turn do? This element addresses adjacency pairs (Schegloff, 2007),
 382 a core structural unit of conversation that can be recursively reproduced and expanded. It consists
 383 of a minimum of two turns by different individuals, where a *first pair part* (e.g., a request) is

384 followed by a predictable response in the form of a *second pair part* (e.g., granting; Pika et al.,
385 2018; Fig. 6).

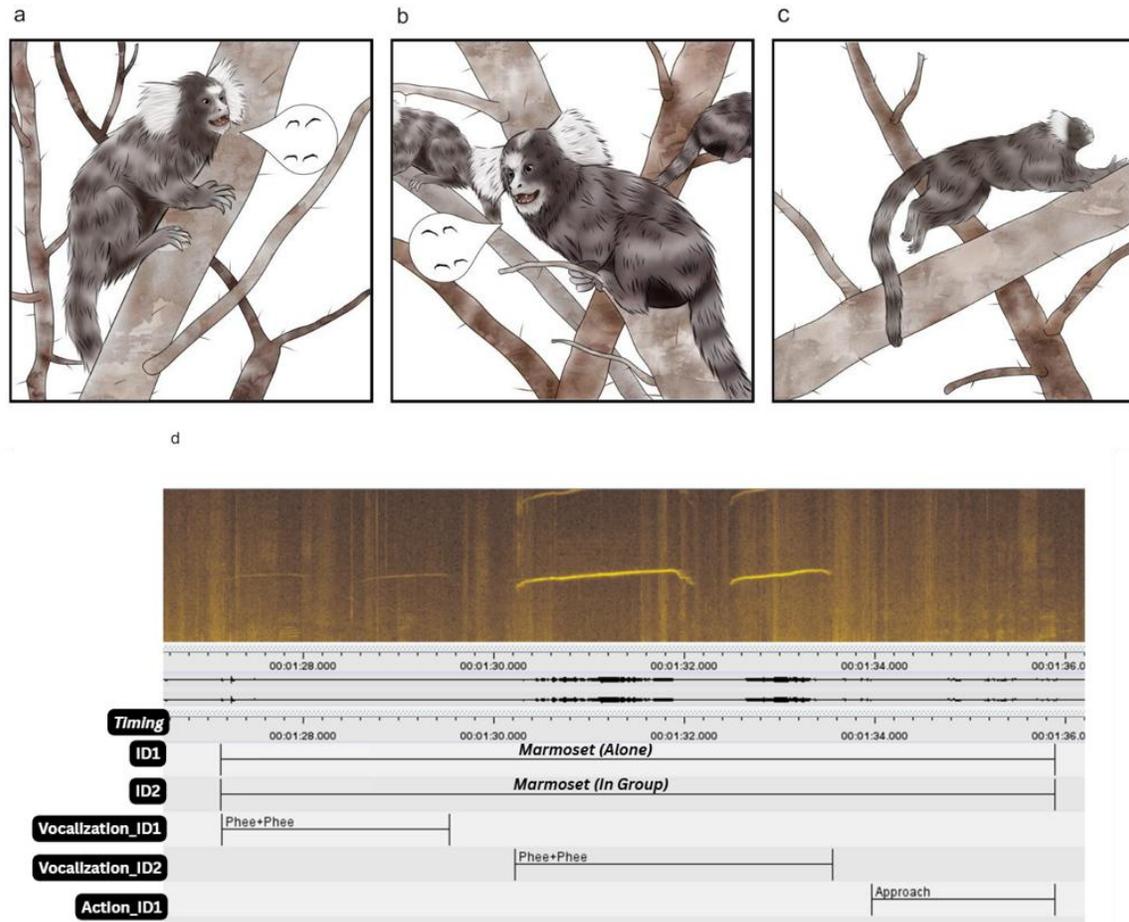
386

387 *Operationalized parameters:* Adjacency pair-like sequences are assessed by quantifying signal-
388 response contingencies, sequential pattern frequencies, and response appropriateness utilizing the
389 following tiers (Table S1): Vocalizations, Gestures, Facial Expressions, Actions. Individual
390 signals/actions are annotated during the annotation phase, while signal-response pairings and
391 sequential patterns are identified post-hoc during the analysis phase, through sequential and
392 collocation analyses that determine contingent non-random associations between:

393 (a) all the adjacent signals/actions produced by participants during the interaction.

394 (b) the sequences employed by the initiator and recipient.

395 *Coding Considerations:* Response appropriateness criteria must be established based on species-
396 specific behavioral repertoires and contextual norms. Sequential analyses should employ statistical
397 methods (e.g., lag-sequential analysis, Markov chain modeling) to distinguish predictable patterns
398 from random associations. Minimum sequence length and timing parameters should be defined
399 based on species-typical interaction dynamics.

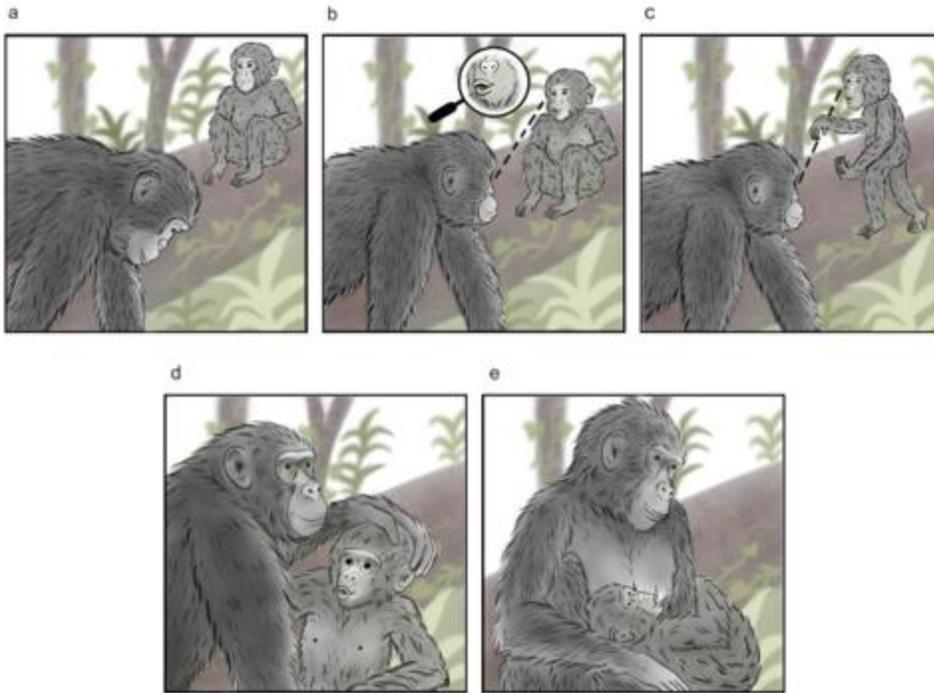


400
 401 *Figure 8.* Adjacency pair-like sequences element in a vocal interaction of common marmosets (*Callithrix*
 402 *jacchus*): (a) ID1 is alone (no visual contact with his conspecifics) and emits a PHEE-PHEE; (b) ID2 from
 403 another group replies with a matching vocalization within 10s; (c) ID1 travels toward the neighboring group
 404 upon hearing the vocalization; (d) ELAN screenshot of the annotated interaction using the tiers from Table
 405 S1. © Luara Martins.

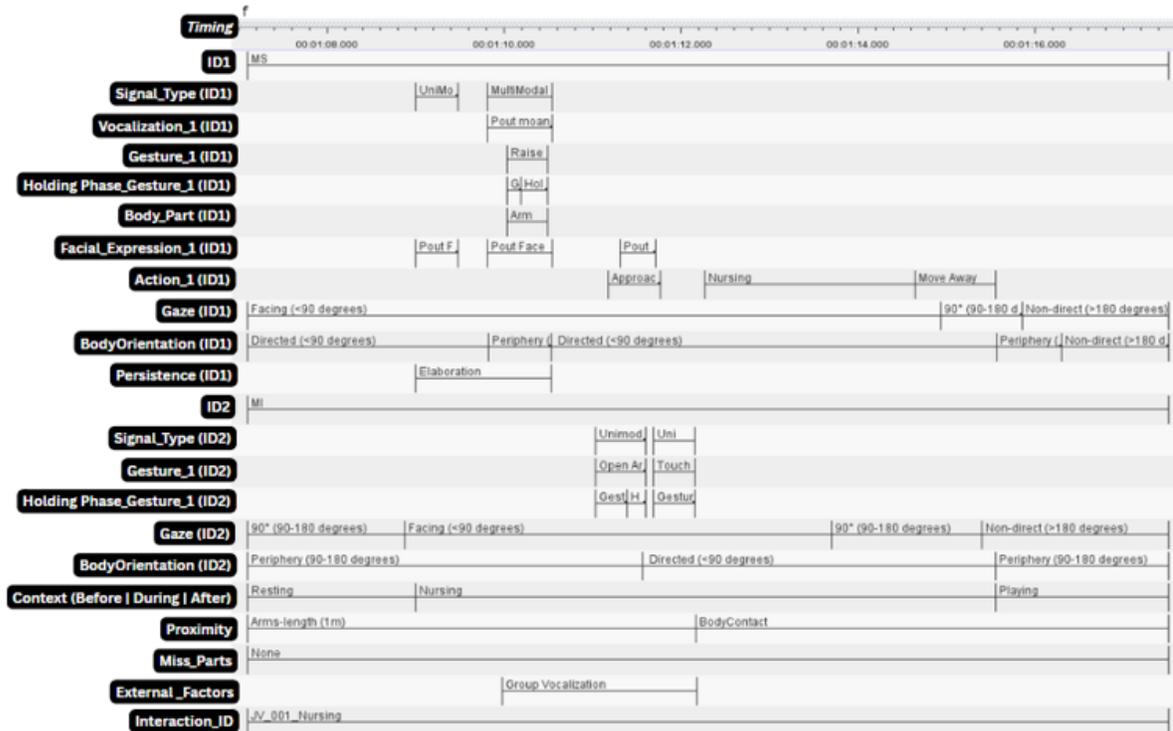
406
 407 **2.4. Integrating Elements: A Bonobo Mother-Infant Communication Example**

408 Here, we aim to illustrate the utilization of our practical toolkit through a detailed example
 409 of a bonobo (*Pan paniscus*) mother-infant interaction, demonstrating how all four turn-taking
 410 elements integrate into a single communicative exchange, and how they can be systematically
 411 annotated using the ELAN annotation software (see Fig. 9 for visual representation and
 412 corresponding annotation screenshot).

413 Consider the following scenario involving an infant requesting to nurse. First, the infant
414 (right) gazes at his mother (left; *Participation framework* – annotated as “<90” in the Gaze and
415 BodyOrientation tiers), and produces a POUT FACE (FacialExpression_ID1; SignalType tier is
416 Unimodal). The mother does not respond (although she looks at the infant; Gaze/BodyOrientation
417 tiers), and the infant elaborates by adding an ARM RAISE (Gesture_ID1 and BodyPart_ID1) and
418 POUT MOAN (Vocalization_ID1) to the POUT FACE (FacialExpression_ID1). These signal
419 combinations and elaboration are part of the *Flexibility* element (Repetition: “Elaboration”;
420 SignalType now: Multimodal). After 0.5s (*Temporal relationships* - offset-onset; see Timing), the
421 mother responds with an OPEN ARM gesture (Gesture_ID2), and allows the infant to access her
422 nipple. This creates an *Adjacency pair-like sequence*: The infant’s multimodal request (POUT FACE
423 + POUT MOAN + ARM RAISE; turn one) receives an “aligning” response from the mother (OPEN ARM;
424 turn two). This triggers further turn-transitions: The infant approaches (Action_ID1), the mother
425 TOUCHES the infant (Gesture_ID2), and the infant nurses (Action_ID1). Additional contextual
426 annotation captures the interaction's full complexity: The Context tier tracks the behavioral context
427 (e.g., resting → nursing (only context visible in Fig. 9.) → playing), the Proximity tier records
428 distance changes (e.g., arms-length → body contact), the Missing_Parts tier indicates data
429 completeness, the External_Factors tier notes influences (e.g., community vocalizations), and the
430 Interaction_ID enables statistical analysis across exchanges. In sum, this systematic annotation
431 demonstrates how our toolkit captures turn-taking complexity within natural communicative
432 exchanges, demonstrating both the depth of information available and its practical implementation



433



434

435 *Figure 9.* All turn-taking elements in a nursing interaction between a bonobo infant (ID1) and its mother
 436 (ID2): (a) ID1 gazes at ID2; (b) when ID2 returns gaze, ID1 produces a POUT FACE; (c) ID2 does not
 437 respond, so ID1 also employs an ARM RAISE and a POUT MOAN in addition to the POUT FACE; (d) ID1

438 responds with an OPEN ARM; (e) the request for nursing has been granted; (f) ELAN screenshot of the
439 annotated interaction using the tiers from Table S1. © Luara Martins.

440

441 **3. Future Directions**

442 Our operationalized turn-taking toolkit advances the study of communicative evolution by
443 shifting the focus from isolated, top-down linguistic categories to a multidimensional, bottom-up
444 analysis of interaction. By integrating and operationalizing the four core elements proposed by
445 Pika and colleagues (2018), we move beyond single elements and modality biases that have
446 historically been applied in this field and have hampered informed comparisons. This bottom-up
447 approach allows to deconstruct complex social exchanges into their fundamental building blocks,
448 such as flexibility and adjacency pair-like sequences, and to identify the behavioral components
449 of cooperation and turn-taking that may have preceded formal language. Crucially, our toolkit
450 highlights that focusing on any single element does not capture the intricate system and involved
451 complexity of turn-taking. For instance, although the temporal rule of overlap avoidance (Sacks et
452 al., 1974), offers valuable insight into timing exchanges, it captures only one dimension of turn-
453 taking and falls short of characterizing the full complexity of human-like conversation
454 (Dingemanse & Enfield, 2024).

455 By broadening the analytical scope to include social actions alongside signals, our toolkit
456 captures the functional logic of interaction that precedes and supports formal language. This
457 comprehensive approach is an essential step for identifying meaningful similarities and differences
458 between animal exchanges and human social action during conversation (e.g., Fröhlich et al., 2016;
459 Habib-Dassetto et al., 2023; Kolff & Pika, 2025; Levinson, 2019; Mondémé, 2022; van Boekholt
460 & Pika, 2025). Furthermore, this multidimensional perspective provides the empirical rigor needed
461 to resolve a longstanding debate: whether fast-paced, extended social exchanges are uniquely
462 human (e.g., Melis et al., 2016; Tomasello, 2010) represent an ancient mechanism characterizing
463 cooperative social interactions found across diverse taxa (Levinson & Holler, 2014; Levinson,
464 2016). Where previous cross-species research has been constrained by methodological
465 inconsistencies and a narrow focus on single modalities (Pika et al., 2018), our systematic toolkit
466 offers the standardized, modality-agnostic metrics necessary for definitive comparisons across the
467 animal kingdom.

468 Although non-human primates remain a favored model system for investigating evolutionary
469 precursors of language and factors triggering its evolution (e.g., Levinson, 2016), our approach
470 stands out by offering the possibility of applying our methodology across a wide range of taxa and
471 communication modalities to allow us to pinpoint exactly which species exhibit organization most
472 akin to human turn-taking, regardless of the modality used. Such comparisons enable us to assess
473 the role of ecological and social factors on communicative abilities and complexity (e.g., group
474 size, cooperation demands, predation pressure) that also may shape turn-taking. Furthermore, as
475 Sacks and colleagues (1974) already noted, humans use multiple turn-taking systems, including
476 those for coordinated actions. Studying these different turn-taking systems in non-linguistic
477 species is the only way to empirically disentangle communication-specific elements of human
478 turn-taking from the general coordination mechanisms shared across social animals, and thus to
479 identify what, if anything, is truly unique to human conversation.

480 Overall, this toolkit enables us to construct a hierarchy of resemblance to human turn-taking,
481 distinguishing between similarities driven by shared ancestry and those arising through convergent
482 evolution (e.g., Henry et al., 2016). For instance, if distantly related species such as crows exhibit
483 turn-taking structures similar to chimpanzees, it may indicate that these behaviors converge
484 functionally rather than reflect a shared evolutionary origin, a distinction with profound
485 implications for understanding the selective pressures that shape communicative complexity.
486 Finally, including interspecies interactions can also further deepen our insight into the fundamental
487 principles of sociality and emergent meaning that transcend strictly linguistic or species-specific
488 norms (Mondémé, 2022). By revealing how turn-taking systems evolve across the animal
489 kingdom, this work brings us closer to answering one of the most fundamental questions in
490 cognitive science: what makes human language - and the social intelligence that underlies it - truly
491 unique.

492

493 **4. Conclusion**

494 In summary, broad comparative analyses will reveal how turn-taking systems evolve and
495 whether they lay the groundwork for more sophisticated communication across the animal
496 kingdom. Our toolkit enables systematic and comparable data collection within and across species
497 and taxa while maintaining analytical flexibility to determine turn-taking presence in their specific

498 contexts. It is important to note that, although all of the presented metrics are valid, researchers
499 should report and specify which metrics were employed for transparency and easier cross-
500 comparisons in the future. Lastly, broadening the scope of turn-taking research will advance the
501 understanding of communication evolution and its interplay with cognition, sociality, and
502 cooperative behavior, moving us closer to unraveling the roots of language.

503

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516 Jolinde Vlaeyen and Filipa Abreu; **Writing – review and editing:** all authors.

517

518 **Data Availability Statement**

519 Data is available at <https://figshare.com/s/c9fe94c30ebad0ed9c7d>.

520 **Conflict of Interest statement**

521 We have no conflicts of interest to declare.

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