

1 Chimpanzee play sequences are structured hierarchically as games

2 Mielke, Alexander^{1,2} & Carvalho, Susana^{1,3}

3 *1 Primate Models for Behavioural Evolution Lab, School of Anthropology and Museum*
4 *Ethnography, University of Oxford, UK*

5 *2 School of Psychology and Neuroscience, University of St Andrews, UK*

6 *3 Interdisciplinary Centre for Archaeology and Evolution of Human Behaviour (ICArEHB),*
7 *Universidade do Algarve, Faro, Portugal*

8

9 **Abstract**

10 Social play is ubiquitous in the development of many animal species and involves players
11 adapting actions flexibly to their own previous actions and partner responses. Play differs
12 from other behavioural contexts for which fine-scale analyses of action sequences are
13 available, such as tool use and communication, in that its form is not defined by its
14 functions, making it potentially more unpredictable. In humans, play is often organised in
15 games, where players know context-appropriate actions but string them together
16 unpredictably. Here, we use the sequential nature of play elements to explore whether play
17 elements in chimpanzees are structured hierarchically and follow predictable game-like
18 patterns. Based on 5711 play elements from 143 bouts, we extracted individual-level play
19 sequences of 11 Western chimpanzees (*Pan troglodytes verus*) of different ages from the
20 Bossou community. We detected transition probabilities between play elements that
21 exceeded expected levels and show that play elements form hierarchically clustered and
22 interchangeable groups, indicative of at least six ‘games’ that can be identified from
23 transition networks, some with different roles for different players. We also show that
24 increased information about preceding play elements improved predictability of subsequent

25 elements, further indicating that play elements are not strung together randomly but that
26 flexible action rules underlie their usage. Thus, chimpanzee play is hierarchically structured
27 in short ‘games’ which limit acceptable play elements and allow players to predict and adapt
28 to partners’ actions. This ‘grammar of action’ approach to social interactions can be valuable
29 in understanding cognitive and communicative abilities within and across species.

30

31 ***Introduction***

32 Animal lives take place in time – actions happen sequentially in response to changing
33 environmental stimuli and the behaviour of other individuals. Particularly in social
34 interactions, each action is a decision based on the social environment, the actor’s previous
35 behaviour, the partner’s reactions, and intended outcomes (Bshary & Oliveira, 2015).
36 Sequential social decisions are therefore an important window into the complexity of animal
37 decision-making abilities (Gygax et al., 2021). Sequences can be considered complex for
38 participants and bystanders if contingencies between actions are increasingly removed in
39 time or with increasing flexibility and decreased determinism of transitions between actions
40 (Kershenbaum et al., 2016). In many animal species, social play involves rapid exchanges of
41 actions between several participants that often appear random to observers, making it one
42 of the most complex social contexts individuals are involved in daily. Multiple individuals
43 combine distinguishable and discrete actions (‘play elements’) in temporal patterns (‘play
44 sequences’) and adapt to partners’ actions. This complexity can provide a unique window to
45 unravel fast-paced decision-making in sequential exchanges between players. However, we
46 currently lack a framework to understand how predictable or flexible play really is.

47 Sequential decision-making processes have been investigated in some detail in tool use and
48 communication. In both, there is increasing evidence for predictable decision-making and
49 hierarchical sequential structures. For example, New Caledonian crows (Hunt & Gray, 2004;
50 Wimpenny et al., 2009) as well as several primate species (Boesch et al., 2020; Carvalho et
51 al., 2008; Deblauwe et al., 2006; Estienne et al., 2017; Hihara et al., 2003; Martin-Ordas et
52 al., 2012) use sequences of steps, often involving multiple objects, to solve problems using
53 tools and tool sets. In chimpanzees, stone tool use (Carvalho et al., 2008; Sirianni et al.,
54 2015), termite fishing (Deblauwe et al., 2006), and digging for underground bee nests
55 (Estienne et al., 2017) have been analysed as complex sequences of individual decisions.
56 Similarly, vocal patterns of bats (Bohn et al., 2009), birds (Berwick et al., 2011; Engesser et
57 al., 2016; Sasahara et al., 2012; ten Cate, 2014), cetaceans (Allen et al., 2019), rock hyraxes
58 (Kershenbaum et al., 2012), and primates (Arcadi, 1996; Arnold & Zuberbühler, 2008; Clarke
59 et al., 2006; Girard-Buttoz et al., 2022; Leroux et al., 2021; Ouattara et al., 2009) have been
60 described as temporal sequences with different degrees of predictability, combinatorial
61 complexity, and hierarchical structure. This has often been related to the evolution of syntax
62 (Zuberbühler, 2019). Increasingly, communication sequences are found for other
63 communicative modalities, such as gestures and facial signals (Aychet et al., 2021; Genty &
64 Byrne, 2010; Graham et al., 2020; Liebal et al., 2004; McCarthy et al., 2013; Safryghin et al.,
65 2021). Studies have shown that Markov processes (i.e., elements are predicted by a finite
66 number of antecedent elements) are insufficient for describing vocal sequences
67 (Kershenbaum et al., 2014). Different species show turn-taking in exchanges and adapt their
68 signals as sequential response to a partner's actions (Demartsev et al., 2018; Fröhlich, 2017).

69 In both tool use and communication research, the form of sequences is defined partially by
70 their function: in tool use, an 'optimal' sequence exists that allows individuals to access a

71 resource (Estienne et al., 2017). In communication, complexity is limited by the need to be
72 understood, which cause sequences to be predictable and short. Songs are not constrained
73 the same way, often containing hundreds of hierarchically structured elements (Berwick et
74 al., 2011). Given that most species do not create song-like vocalisations, understanding
75 sequences in social interactions (their 'grammar of action'; Pastra & Aloimonos, 2012) could
76 potentially allow for a broader perspective on action sequences. Play is a prime candidate
77 because the form of play is not necessarily the results of a specific function – play has been
78 hypothesised to have evolved as practice for future challenges facing individuals, so it is
79 defined by its unpredictability compared to 'real' interactions (Fagen, 1981; Palagi et al.,
80 2004; Smith, 1982).

81 Play behaviour, at least during some parts of development, is common in most mammals
82 and birds (Diamond & Bond, 2003; Fagen, 1981), and exists in some reptile, fish, and
83 amphibian species (Burghardt, 2015) and in octopuses (Kuba et al., 2006), indicating that it
84 is an ancient behavioural context. Species can have large repertoires of distinct elements
85 (Petrů et al., 2009). Play signals are deliberately used to prevent play from breaking down
86 when intentions are unclear or risk is high (Cordoni & Palagi, 2012), and extend the length of
87 play bouts (Waller & Cherry, 2012). We have yet to learn how coordinated other play
88 actions are, and whether expected responses to certain action sequences are socially
89 learned or innate. In human play, there are specific, socially learned arbitrary rule systems
90 that govern what we call 'games' (Leisterer-Peoples et al., 2021): in a game, certain actions
91 and sequences are allowed or not, but their order can be flexible. For example, in hide-and-
92 seek, hiding is allowed, but laughing loudly is counterproductive, where and how to hide is
93 up to the player. There is evidence that apes have standardised games and play them with
94 each other and human partners (Costa et al., 2019; Pika & Zuberbühler, 2008; Tanner &

95 Byrne, 2010) – however, these examples focus on special contexts (e.g., playing in water,
96 playing socially with objects), and we do not have a method to determine how widespread
97 predictable behavioural rules are.

98 The Bossou Western chimpanzees (*Pan troglodytes verus*) have been studied since 1976
99 (Matsuzawa & Humle, 2011). An ‘outdoor laboratory’ was created in 1988 as a clearing in
100 the territory of the community where stones and nuts are provided to study tool use, with
101 standardised video recordings available for over 30 years. Because the chimpanzees spend
102 considerable time there, social and object play can be observed regularly (Myowa-
103 Yamakoshi & Yamakoshi, 2011). In chimpanzees, infants and juveniles play more than older
104 subadults and adult individuals (Cordoni & Palagi, 2011), but chimpanzees are among the
105 few species where adult play seems common (Fernandez-Duque et al., 2000) and fulfils
106 several functions, especially in conflict regulation and stress reduction (Palagi et al., 2004).
107 Chimpanzees play with and without objects (Koops et al., 2015), and solitary and socially,
108 often involving more than two players (Cordoni et al., 2018; Shimada, 2013). Play signals are
109 used to advertise willingness initiate play bouts and increase their duration (Davila Ross et
110 al., 2009; Matsusaka, 2004; Waller & Dunbar, 2005), and there is good evidence that
111 chimpanzees show matching or mimicry of partners’ play face and laughter (Davila-Ross et
112 al., 2011; Ross et al., 2014). Gestures can occur in sequences during play (Bard et al., 2014),
113 especially if partners fail to respond initially, with tactile and audible gestures usually
114 occurring early in the sequence (McCarthy et al., 2013) and younger individuals producing
115 more tactile gestures (Fröhlich et al., 2016). The cooperative and coordinated nature of play
116 (multiple individuals adapting their behaviour in real-time to sustain the interaction) has
117 been used to study higher socio-cognitive skills such as joint intention and shared
118 intentionality with varying results (Bekoff & Allen, 1998; Pika & Zuberbühler, 2008;

119 Tomasello et al., 2005), and joint commitment and joint action (Heesen, Bangerter, et al.,
120 2021; Heesen et al., 2017; Heesen, Zuberbühler, et al., 2021). Anecdotal evidence from the
121 Bossou chimpanzees has repeatedly indicated that chimpanzee play might involve aspects
122 of pretence or imagination (Matsuzawa, 2020; Nakamura, 2012). Our focus is on the form of
123 play, how elements are strung together, which has its own implication for cognitive
124 evolution.

125 For this study, we tested whether sequences of play elements are predictable for players or
126 contain a large amount of randomness, and whether we can identify hierarchical structure
127 in sequence patterns. To do this, we ask two main questions: if I know the previous action
128 ('antecedent'), can I predict the subsequent action ('consequent')? And are there higher-
129 order connections between elements, in the form of network clusters of interchangeable
130 elements? This last aspect would indicate the presence of 'games': once we are playing a
131 game, certain elements are permissible, but their order and exact usage can vary. This study
132 specifically looks at transitions within individuals - partner behaviour is considered 'noise'.
133 This will reduce predictability, because actions that appear 'unexpected' here are possibly
134 expected responses to partner actions. We hypothesize that some play elements are
135 consistently more likely to follow specific antecedents than would be expected at random.
136 Using the probabilities of each element and each transition to 'predict' which element will
137 appear next, we expected classification accuracy that exceeds random assignment, and that
138 higher-order sequences (AB, rather than B alone, to predict C) further improved prediction
139 accuracy. We also hypothesized that, like communication in some species (Allen et al.,
140 2019), we can detect hierarchical structures in transition networks ('games') as clusters of
141 elements that are often used together and can be used interchangeably. Using the
142 transition probabilities of each element to each other element, we can identify clusters of

143 elements that have similar transition patterns (i.e., act like ‘synonyms’). The network
144 structure allows us to identify elements that were essential to a game (in the sense that
145 they occurred at higher rates than other elements in the cluster and connected other
146 elements in the sequence; Carvalho et al., 2008). Lastly, we predict that the similarity and
147 transition clusters overlap – i.e., we have clusters of elements are interchangeable and
148 tightly linked in time.

149

150 **Methods**

151 *Sample*

152 We scanned 116h of video material from the Bossou video database (Matsuzawa & Humle,
153 2011), collected between 2009 and 2013. While footage from the Bossou outdoor lab has
154 high video quality and filming consistency, the social composition of the group limits
155 generalisability. The Bossou community at the time was small (around 13 individuals)
156 (Matsuzawa & Humle, 2011). Due to the age distribution, there was only one infant, one
157 juvenile, and one subadult individual in the group during data collection – making it difficult
158 to differentiate between age effects and individual preferences (Fröhlich et al., 2016).
159 Eleven individuals were observed playing at least once; however, the distribution of
160 observations was highly skewed, with the two juvenile/subadult players each participating
161 in about 75% of all play bouts, while none of the adults participated in more than 20% of
162 play bouts. Thus, most play elements and transitions were provided by two individuals,
163 often playing with each other. In this study, we do not control for individual or age
164 differences in play behaviour and sequences, due to the limited sample. These could make
165 play transitions more predictable (individuals or specific age groups might have

166 standardised ways of reacting that other group members know). Considerably more data
167 would be necessary to control for individual- or dyad-level effects in transition patterns. We
168 identified 143 bouts of social play across 35 videos - defined as play involving at least 2
169 individuals, with a new bout started if both individuals stopped playing for at least 5 seconds
170 continuously. Bouts consisted of between 3 and 181 individual play elements (mean = 30.3),
171 including between 2 and 4 players at any given time. For analyses, the bouts were split into
172 individual-level bouts (every play element an individual performed during a bout), resulting
173 in 306 individual-bouts.

174 *Coding Scheme*

175 The coding scheme, with detailed definitions of all play elements and coding conventions
176 can be found in the associated repository. Potential play elements were identified from
177 several sources – primarily, every behaviour indicated in Nishida et al., (2010) as potential
178 play behaviour, the literature on ape gestural repertoires (Genty et al., 2009; Graham et al.,
179 2017; Hobaiter & Byrne, 2011, 2014), previous chimpanzee play literature (Fröhlich et al.,
180 2016), and descriptions of play elements in primates more widely (Petrú et al., 2009). Often,
181 these sources use different terms for similar play elements, and the definitions used here do
182 not always overlap perfectly with those used previously. To our knowledge, the ethogram
183 used here is the most detailed ethogram for chimpanzee play to date. Play elements can
184 roughly be categorised as contact or non-contact, and as events (countable, one-off or
185 repeated actions) or states (continuous behaviour with a clear start and end point). Social
186 object play formed its own category, with multiple different ways of interacting with
187 detached objects (mainly stones, nuts, and sticks) available. In total, our ethogram
188 contained 118 different play elements, of which 106 were observed at least once. We

189 assumed that the elements we defined are meaningfully different from each other. This
190 might not be the case: the difference between *Retreat* (walking away from partner), *Flee*
191 (running away from partner), and *Retreat Backwards* (walking away from partner while
192 looking at them) might be an artifact of the coding scheme.

193 Coding was done using BORIS v.7.9 video coding software (Friard & Gamba, 2016). We
194 coded bouts one player at a time and marked the start of every change in play element and
195 mark all active play elements at that time point. For example, if an individual goes *bipedal*,
196 this is marked. If, while bipedal, the individual approaches the partner, we would mark
197 *bipedal/approach*. If they would then raise their arm while performing those actions, we
198 would mark *bipedal/approach/arm raise*, and so on. This leaves us with a string of play
199 elements with a time stamp for initiation. If any player stopped playing (i.e., no play element
200 was active), a Break was coded. The duration of play elements was available but was not
201 considered in this study – we focus entirely on the sequential order.

202 Video coding of entire play bouts is slow, due to fast changes of behaviour and movements,
203 and researchers usually focus only on play initiation and re-initiations (Heesen, Bangerter, et
204 al., 2021; Hobaiter & Byrne, 2011). Due to the challenges of this detailed coding approach,
205 no inter-rater reliability was performed, and results must be viewed with this limitation.
206 Predictability should be higher in studies using simpler coding schemes, so if we can show
207 high predictability using the current ethogram, we have taken the conservative approach.
208 The dataset currently contains 5711 play elements. Where possible, we present results
209 including uncertainties, and used permutation and bootstrapping approaches to
210 discriminate between spurious and reliable transition patterns.

211 *Pre-processing*

212 All pre-processing and analyses were conducted in R statistical computing software (R
213 Development Core Team & R Core Team, 2020). The video coding data needed pre-
214 processing to deal with three main problems inherent to the coding process: rare elements;
215 some artificially common elements; and establishing the sequential order of co-occurring
216 elements.

217 To robustly establish probabilities of transitions between elements, rare elements are a
218 problem (Silge & Robinson, 2017). For example, if an element only occurs three times, and
219 each time transitions into a different element, we do not know if the high transition
220 probability would disappear with increasing sample size. We set the threshold at 20
221 occurrences per play element. However, removing these cases completely (as is often done
222 in linguistic studies; Silge & Robinson, 2017) would be wasteful given the sample size of this
223 study. For most play elements, we defined *a priori* with which other play element they
224 would be combined if too few occurrences were observed (see associated repository).
225 Replacement elements were chosen based on similarity of movement. If the combination
226 after this lumping process failed to reach the threshold, we nevertheless retained it. Thus,
227 our rarest element had 9 occurrences (see associated repository for occurrence probabilities
228 of all play elements before and after pre-processing). After this step, 68 play elements
229 remained.

230 Some elements occurred at much higher frequencies than others. The seven most common
231 elements (Bipedal, Hold, Follow-Other, Approach, Retreat-backwards, Retreat, Flee) were all
232 coded continuously and therefore were noted every time a change occurred while they
233 were active. Imagine a musical piece on the piano: sometimes one note is held while others
234 are played. In play, a chimpanzee could go bipedal, but then perform other actions while

235 the *Bipedal* was marked at every change in event. These elements potentially skew
236 transition probabilities and mask transitions between other elements. Ideally, we want a
237 sequence that reflects when individuals made the choice to use a specific element. We
238 addressed this by detecting cases where one of those seven elements occurred multiple
239 times in a row, and only retained the first case. If players stopped the continuous action
240 (e.g., stopped fleeing, then started again), the element was counted again.

241 In play, it is possible to go *Bipedal*, *Arm Swing* with one arm and *Hit* the partner with the
242 other arm. This is problematic in terms of the transitions - does *Bipedal* lead to *Arm Swing*;
243 or *Arm Swing* to *Bipedal*? This problem also occurs mainly because some elements (e.g., *Flee*
244 or *Bipedal*) are continuous states, while others (e.g., *Kick*) have a clearly defined beginning
245 and end. We used permutations – randomly assigning order within co-occurring elements
246 and repeating all analyses 1000 times with different orders – as there was no *a priori* reason
247 to assign primacy to one co-occurring element over another. Thus, all described transition
248 probabilities are averages over multiple permutations, which is why transition counts are
249 not integers. Two alternative approaches (random sampling of only one of the co-occurring
250 elements, bag-of-words) can be performed using the attached R scripts and generally
251 showed similar results.

252 *Transition Probabilities*

253 The transition probability between antecedent and consequent were defined by the number
254 of times the consequent followed the antecedent, divided by the number of times any
255 element followed the antecedent (conditional probability). The antecedent could be a single
256 element (used to establish first-order n-grams, networks, and transition similarities), but
257 also n-grams of different order (e.g., first order: *Hit*; second order: *Hit/Slap*; third order:

258 *Hit/Slap/Tickle* etc). The latter approach was taken to determine whether increased
259 information about antecedents increases prediction accuracy. Current sample size prevents
260 us from analysing long sequences, as the number of possible transitions increases
261 exponentially with each new level. We limited the analyses to a maximum of 3 antecedent
262 elements. We restricted ourselves to one-element consequents and did not consider non-
263 adjacent contingencies (Sonnweber et al., 2015).

264 The large number of possible combinations combined with a small dataset and the small
265 number of individuals leads necessarily to overfitting: some combinations will only occur a
266 few times and adding new information could influence our understanding of their function.
267 We did two things to counter this: rare elements were combined, as described above.
268 Where possible, we report some measure of robustness to give the reader an understanding
269 of how reliable results were. Robustness was established using bootstrapping procedures –
270 randomly selecting 1,000 subsets of the data and establishing transition probabilities within
271 those subsets.

272 *Randomisation Procedures*

273 To test which elements followed which antecedent, we created a null model of ‘expected’
274 transitions using permutations of observed patterns. We chose this resampling approach
275 over collocation analysis (Bosshard et al., 2021) to account for the regular co-occurrence of
276 play elements that is usually not seen in single-modularity communication. We repeatedly
277 randomized the order of elements across bouts: while the number of elements per bout,
278 the probability of elements to occur across bouts, and the position of Breaks and missing
279 data in each bout were kept the same, we randomly assigned element positions. Thus,
280 transitions are considered significant if they were observed more often than would be

281 expected if play elements were just strung together randomly given their base probabilities.
282 We ran 1000 randomisations to create the expected distribution for each transition and
283 compare whether the observed transition probability fell within this distribution or not. To
284 compare the observed and expected values, we provide a p-value (how many of the 1000
285 randomisations show higher transition probabilities than observed; Mielke et al., 2021). We
286 report transitions that occurred at least five times and that were significant at 0.01 level
287 (i.e., the observed value was higher than for 990 permutations). These calculations also
288 constituted the basis for the network clusters described below.

289 *Prediction Accuracy*

290 To understand the predictability of transitions rules, we applied the probabilities derived
291 from a subset of the data to 'unknown' test data and explored how well the former
292 predicted the latter (Chollet & Allaire, 2018). We tested the predictability of elements within
293 bouts by calculating transition probabilities for 95% of all other bouts, then predicting each
294 element in the remaining 5% of bouts based on their antecedents (k-fold validation). This
295 was repeated 1,000 times per bout. We tested the expected correct classification if the
296 consequent element was only determined by base occurrence probabilities (null model).
297 The difference between this value and the observed prediction accuracy of the models tells
298 us how much knowledge of the antecedent increases our predictions. Aside from using one
299 element as antecedent (describing a simple Markov process), we repeated the process with
300 two or three elements as antecedents (n-gram prediction; (Eisenstein, 2019). For higher-
301 order antecedents, the probabilities of the lower-order antecedents were combined
302 (interpolation) – therefore, for *Approach/Stare At/Hit* as third-order antecedent, the
303 probability is the product of the probabilities of the triad, *Stare At/Hit*, and *Hit*. This was

304 done because many higher-order antecedents only occurred infrequently, and no
305 information would otherwise be available as to which consequent was appropriate. For
306 transitions that were never observed, Laplace smoothing was applied, assigning them one
307 occurrence, and adapting all transitions accordingly (Eisenstein, 2019). If the prediction
308 accuracy under those conditions was higher than for one element, this indicated hierarchical
309 processes - for example, if *Hit* correctly predicts to *Hold* 10% of the time, but *Stare*
310 *At/Hit* leads to *Hold* in 80% of the time, then the sequence order added information. We
311 present the mean correct classification rate across all bouts and elements. In addition to
312 predictions based on the transition probabilities, we implemented a naïve Bayes classifier
313 using the 'e1071' package in R (Meyer et al., 2021). Naïve Bayes classifiers use vectors of
314 feature values (in our case, the previous play element, two previous play elements, etc.) to
315 predict the correct consequent using Bayes theorem (Eisenstein, 2019). Using an established
316 classifier offers the advantage that classification is optimised and faster than the above-
317 described prediction based on raw transition probabilities. However, naïve Bayes classifiers
318 make a strong independence assumption, effectively assuming that the antecedents are
319 independent from each other given the consequent class (Eisenstein, 2019). Therefore,
320 while increased performance of the classifier with increasing number of antecedents would
321 indicate that information about previous play actions increases predictability of what
322 happens next, performance cannot be interpreted as based on sequential information.

323 *Similarity*

324 We determined whether there were play elements that resembled each other in which
325 elements followed them and tested whether we could find clusters of similar elements. This
326 is similar to the identification of synonyms in language (Levshina, 2015), and we did it both

327 to test whether our assignment of distinct elements during coding was meaningful and to
328 see whether there were clusters of interchangeable elements. Each element was
329 represented by a vector of transition probabilities with all elements. We applied Uniform
330 Manifold Approximation and Projection (UMAP; McInnes et al., 2018) to achieve two-
331 dimensional representation for each vector using the ‘umap’ package (Konopka, 2022). We
332 established similarity between play elements by calculating the Euclidean distances
333 between UMAP projections. To identify the optimal number of clusters for the hierarchical
334 clustering, we used K-Means clustering as implemented in the ‘cluster’ R package (Maechler
335 et al., 2022) to determine a) the optimal number of clusters, and b) the quality of the cluster
336 solution. We present the silhouette value (Rousseeuw, 1987) to detect the best cluster
337 solution, indicating an acceptable distance between clusters and coherence within clusters –
338 any solution above 0.3 can be considered to show that there is more similarity within than
339 between clusters. As cluster solutions differ based on the outcome of the UMAP dimension
340 reduction, we repeated the dimension reduction and cluster detection 50 times with varying
341 numbers of epochs for the UMAP (on average 7000 epochs) and continue using the most
342 likely cluster solution. We plot the dendrogram for the optimal cluster solution and saved
343 cluster memberships for later comparison with network clusters.

344 *Networks*

345 Networks can be useful tools to visualise the connections between elements in
346 communication networks and to identify clusters of elements that have above-expected
347 connections with each other (Allen et al., 2019; Aychet et al., 2021; Barceló-Coblijn et al.,
348 2017; Mielke et al., 2021; Weiss et al., 2014). Here, we created a network using all play
349 elements as nodes and the transition probabilities between them as edges (Newman, 2010).

350 Only transitions that were significantly more likely than expected and occurred at least 5
351 times, to make the network intelligible despite the large number of elements and ensure
352 biological relevance. Edges were weighted, representing the transition probabilities
353 between elements; and directed, meaning that each dyad of elements was represented with
354 two values (A to B, B to A). We used the 'igraph' and 'ggraph' R packages (Csardi & Nepusz,
355 2006; Pedersen, 2021) to create and visualise networks. To test whether distinct 'clusters' of
356 play elements existed in the network (indicating groups of play elements that have strong
357 connections with each other but weak connections to the outside), we used the
358 'cluster_optimal' community detection algorithm in igraph, which maximises modularity of
359 clusters (Csardi & Nepusz, 2006). Clusters were considered to represent stronger
360 connections within than between clusters if the modularity value of the cluster solutions
361 was larger than 0.3. Cluster solutions were compared to those produced by the similarity
362 measure above.

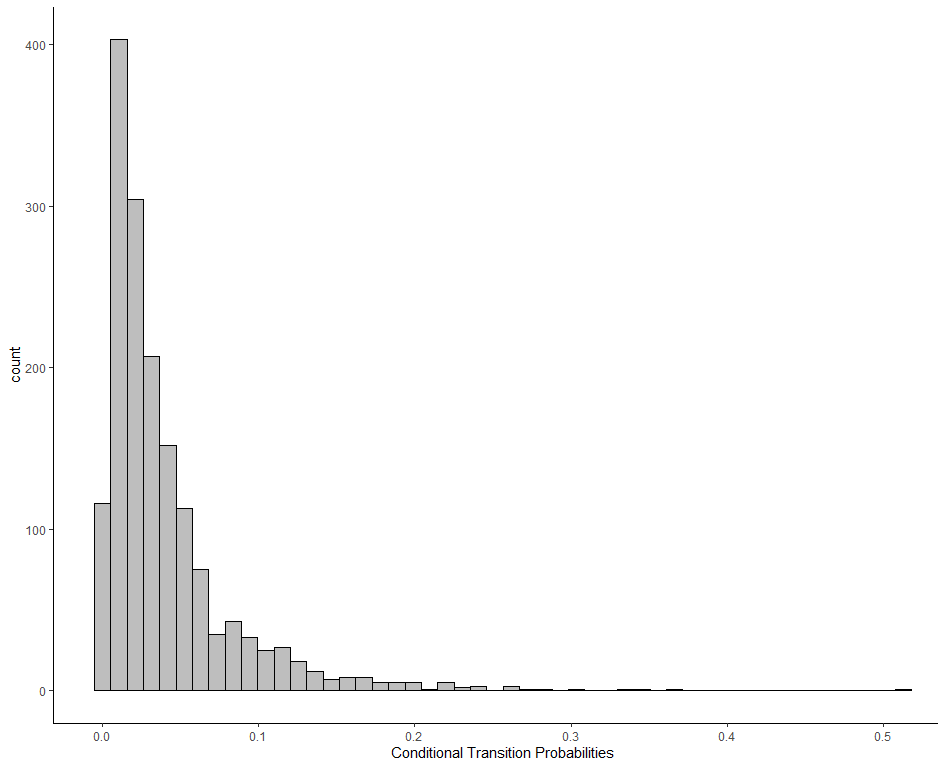
363

364 **Results**

365 *a) Non-random transitions*

366 There were 1622 transitions that were observed at least one time. The histogram (Fig. 1)
367 shows that most elements are followed by several different consequents with low
368 probabilities. In only 4 cases did a consequent constituted more than 30% of all possible
369 transitions of an antecedent, with two of those (Drum Tree and Kick Dirt) being loops – the
370 element was repeated sequentially. At the same time, each element was observed to be
371 followed by between 7 and 53 elements. Thus, there was no tight coupling between any two
372 elements. This might indicate random assignment - any elements could be followed by any

373 other. However, it might also mean situation-specific responses that were tailored to the
374 players' own previous action and the partners' reaction, or predictability at a higher order
375 (e.g., based on multiple antecedent).

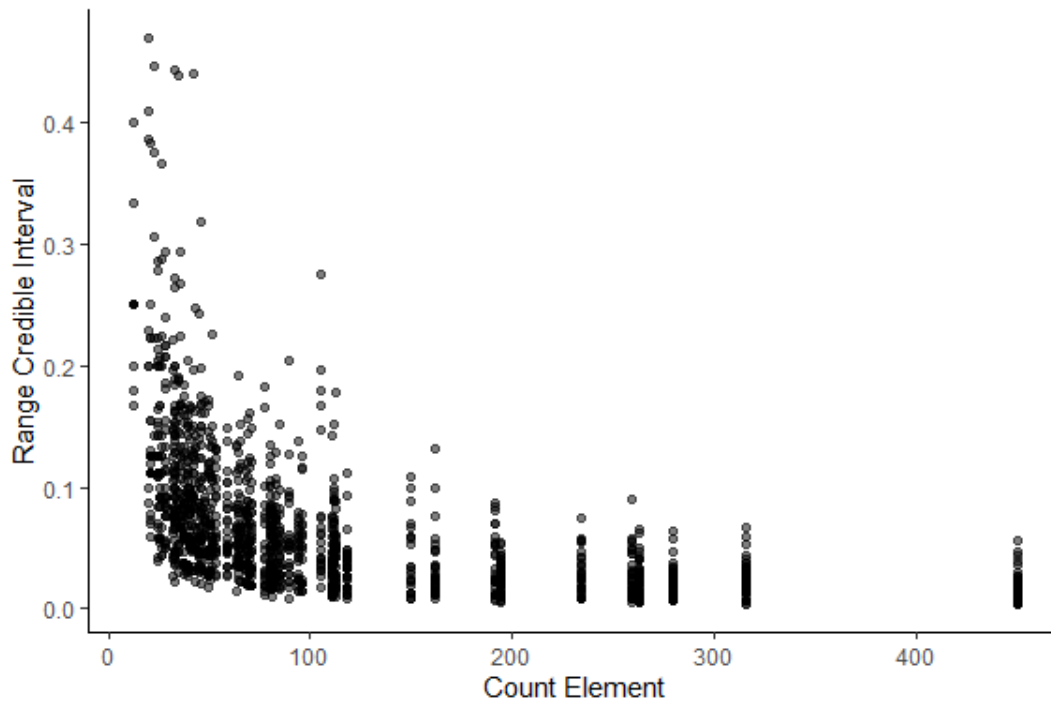


376

377 *Figure 1: Transition probabilities for each simple antecedent - consequent pair*

378 We also visualize how robust transitions were (Fig. 2). Using bootstraps, we created an
379 interval around the observed transition probabilities. We plotted the range of values for
380 each transition for the 1,000 bootstraps (calculated as the highest transition probability
381 minus the lowest transition probability of A to B in the set) against the number of times the
382 antecedent was observed. For some rare elements, transition probabilities remained
383 volatile. Transition probabilities of rare elements therefore must be interpreted with
384 caution, and elements will be filtered to exclude rare transitions – in all descriptions of

385 'significant' transitions and in the networks, only transitions that occurred at least 5 times
386 were considered and reported.



387

388 *Figure 2: Range of bootstrapped transition probabilities compared to the occurrence of the*
389 *antecedent. Transitions of rare antecedents are volatile.*

390

391 In total, 146/1622 transitions (9 %) were significantly more likely than expected. More
392 detailed depictions of these patterns can be seen in the network below and in the
393 associated repository. When analysing the non-random transitions in detail, we found that
394 many elements significantly followed themselves (21 out of 147 significant transitions).
395 Several of the elements used here – for example, rocking or drumming on an object – are
396 repeated actions and each occurrence was marked as independent event. In contrast to all
397 observed transitions described above, many elements (17/68 elements) had no significant
398 consequent, 14/68 had only one significant consequent, with the maximum number of

399 significant transitions in one antecedent being 10 consequents (for *Holding* the partner and
400 *Bipedal*).

401

402 *b) Next-element predictions*

403 When applying the transition probabilities as predictions, increased information about
404 antecedents increased predictability (Tab. 1). The basic probability of correctly predicting an
405 element based on its occurrence probability (zero-order) was 0.03. By applying the
406 probability of one antecedent (unigram; e.g., *Hit*) we increased the probability to 0.06 –
407 almost a doubling of correct classification. When adding two antecedents (bigram; e.g.,
408 *Bipedal/Hit*), there was another rise to 0.11 – again, almost a doubling of correct
409 classifications, and almost four times higher than having no information about antecedents.
410 At the third order, we do not achieve further improvement. For the naïve Bayes classifier,
411 using a more optimised approach that however assumes independence of antecedent
412 elements, we achieve correct classification results of 0.09 as baseline, 0.13 for the first
413 order, 0.25 for the second order, and 0.31 for the third order. Thus, additional information
414 about preceding elements improved prediction accuracy. However, there was still a lot of
415 unexplained variation.

416 *Table 1: Correct prediction ability of consequent elements based on antecedents of different*
417 *orders for the probability distribution and naïve Bayes classifier*

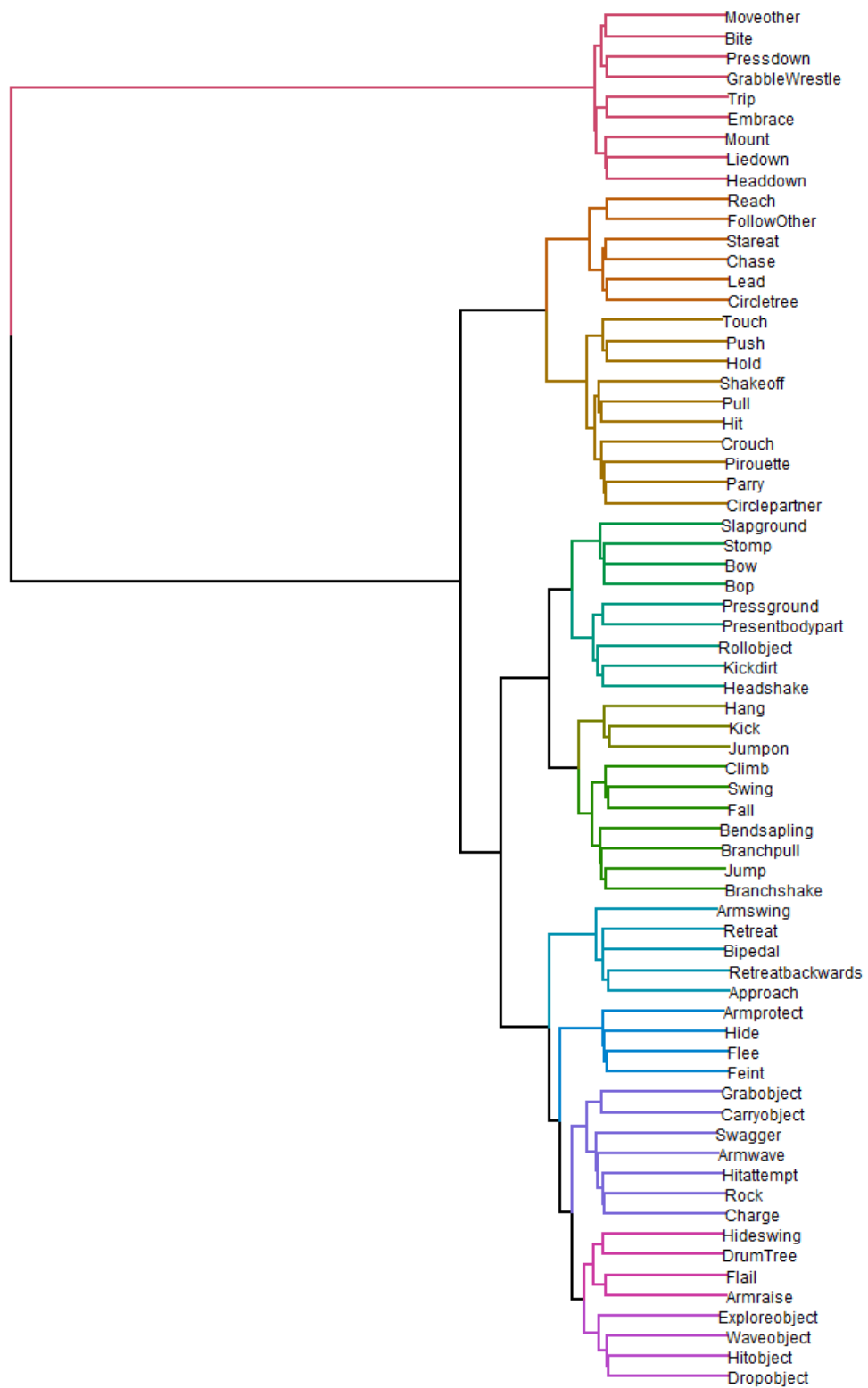
Order	Antecedent Example	Accuracy Probability	Accuracy Naïve Bayes
0	-	0.030	0.086
1	Hit	0.057	0.153
2	Stare At/Hit	0.105	0.247
3	Approach/Stare At/Hit	0.105	0.308

418

419 c) *Similarity between elements*

420 In Figure 3, we can see the dendrogram representation of hierarchical clusters of distances
421 between transition probability vectors of all play elements. Elements connected through
422 shorter branches and assigned the same cluster membership (same colour of branches) are
423 considered more similar than those further away and with different colours. The best cluster
424 solution, with silhouette value of 0.68 (indicating a well-distinguished cluster solution)
425 contained 12 clusters. The cluster allocation can be seen in Table 2, and we will discuss their
426 potential classification together with the network. What we can see here is that there were
427 many elements that were similar in consequents. For example, *Kicking* the partner and
428 *Jumping on* them were close, indicating that they could have been defined as a single play
429 element. Similarly, *Retreating Backwards* and *Retreating* were closely connected. A lot of
430 similarity between elements can be explained by their frequent co-occurrence – for
431 example, *Retreat* and *Bipedal* showed high similarity because chimpanzees often retreat
432 from the play partner while bipedal.

433



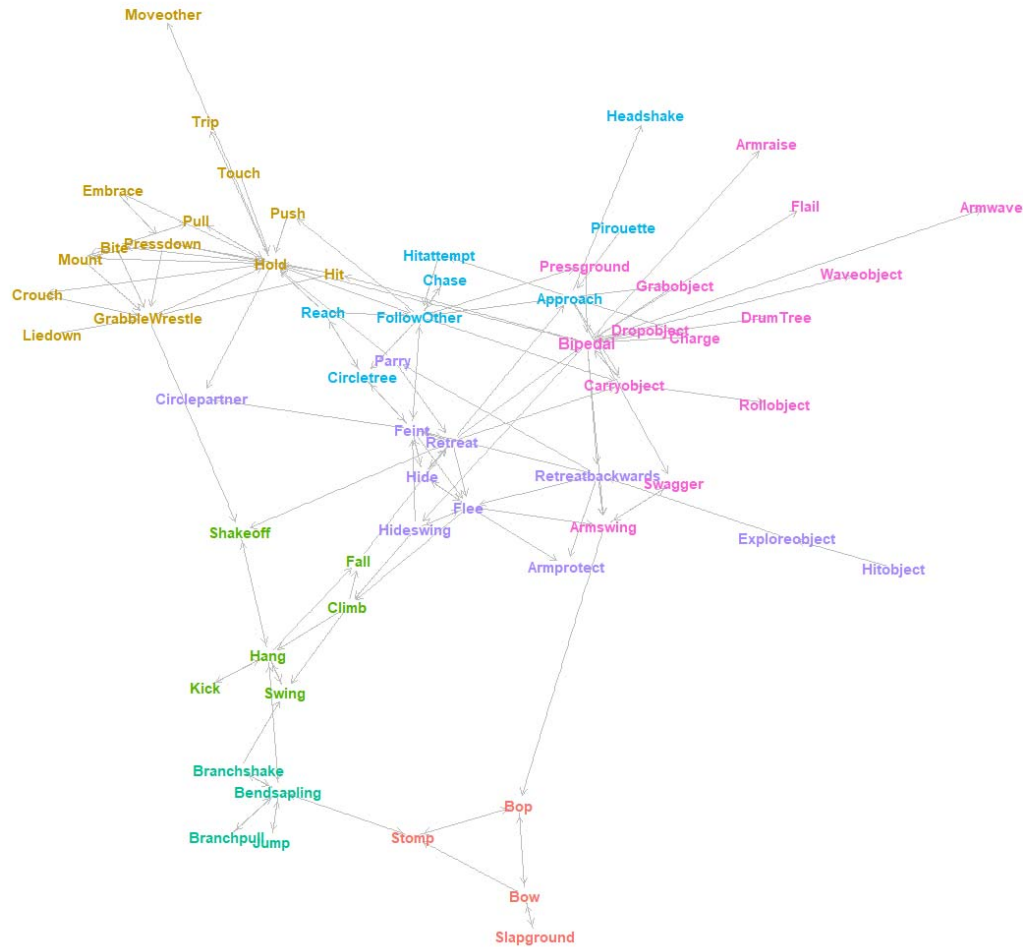
435 *Figure 3: Dendrogram of hierarchical clustering of distances between play elements. Branch*
436 *colours indicate established cluster membership. Optimal cluster solution: 11 clusters.*

437 *d) Network structure*

438 In contrast to the similarity clusters, which assess whether two elements are used at similar
439 points in a sequence, the transition network (Figure 4) describes which consequent follows
440 which antecedent. The network only depicts transitions that occurred at higher-than-
441 expected rates and occurred at least 5 times in the dataset. Colours indicate community
442 membership. As the high modularity of the network community detection algorithm
443 (modularity = 0.65) indicates, there were seven clearly distinguished communities in the
444 network. If community assignment was random, we would expect around 32% of transitions
445 between the elements within communities, but we observed 48% of transition within
446 communities – a 1.5-fold increase. Connections between communities were often due to
447 elements that can be used in different situations. For example, *Shake Off* is used when
448 playing *wrestling* with a partner to get away, but equally when the player is *hanging* off a
449 branch or *retreating* – hence, the element is connected to three communities. Individuals
450 *stomp* when initiating play in combination with *Bop* and *Bow*, but also when they were
451 *bending* a small tree and holding onto it.

452

Transition Network Play Elements; Modularity = 0.65



453

454 *Figure 4: Network plot of weighted transition probabilities between play elements. Play*
455 *elements are nodes, significant transitions that occur at least 5 times are edges (directed),*
456 *and colour indicates cluster membership.*

457 For the interpretation of communities, in combination with the similarity clusters, see Table
458 2. There was considerable overlap between the two approaches, with small variation arising
459 mainly because several elements did not have any significant transitions above threshold
460 level, and the combination of object-related and movement elements resulted in overlap
461 between the chase and object clusters. The different cluster combinations ('games') can be

462 categorised broadly by whether they involved climbing by either partner, had physical
463 contact, involved chasing, involved objects, or were play invitations. For the latter, one clear
464 cluster emerged, consisting of *Bop*, *Bow*, *Stomp*, and *Slap Ground*, which individuals often
465 combined and repeated in quick succession to indicate that they were willing to play. Some
466 other, rarer elements (*Present Body Part*, *Rock*, *Kick Dirt*, *Stare At*) can fulfil a similar
467 function. Play elements routinely used when one or both individuals were in a tree
468 transitioned into each other at high rates, depending on the role of the focal individual.
469 When the player was on the ground and the partner in the tree, individuals would often
470 *bend the tree* (the most central element of this cluster), and then *pull* or *shake* it, sometimes
471 while *jumping*. While players were in the tree, they *climb* up and then *hang* while *swinging*,
472 *kicking* the partner, *shaking them off*, and ultimately *falling*.

473 Most contact play formed one large community in the network, with elements transitioning
474 into each other at high rates. Based on the similarity of transition probabilities, we could
475 differentiate two groupings: contact play that involves players to stay in one spot (*Bite*,
476 *Wrestle*, etc), centred on *holding* the partner in place; and those that involve one player
477 trying to get away from their partner while still in contact (*Push*, *Trip* etc).

478 The different object-related play elements were connected, including detached objects and
479 trees. Chimpanzee players held onto objects once they had grabbed them and then
480 manipulated them in different ways. Object contact was the defining element of this type of
481 play. A common way for the Bossou chimpanzees to initiate play with object contact was to
482 *roll objects* towards the partner or *press the ground*. Individuals will often *drum trees*. After,
483 players regularly *hide swing* (swinging around a tree at speed), which will lead to tree play
484 after. Players *wave objects* about while *swaggering* towards the partner and *flailing* or

485 *waving* their arms. Many of the social object elements were connected to *retreating*
 486 movements, with the player retreating while holding an object, which explains the
 487 community overlap of object interactions and avoidance movements.

488 The remaining cluster combinations were related to chasing play on the ground. Again, we
 489 can identify different roles of the player: One community were those elements strongly
 490 connected to movements used to avoid the partner *retreating* or *retreating backwards* from
 491 them and *hiding* behind trees or *feinting* directional changes, often lifting their *arm*
 492 *protectively*. They will *circle the partner* while *parrying hits*. The last cluster combination
 493 involved the opposite, with the individual *approaching* the partner (sometimes following a
 494 *pirouette* as play initiation, often combined with *bipedal* movements and *arm swings*),
 495 *chasing*, and trying to make physical contact while the partner flees (*Reach, Hit Attempt*).

496

497 *Table 2: Play elements with their cluster/community assignment for both the similarity and*
 498 *network of transition probabilities*

Play Element	Similarity Cluster	Network Community	Game Description
Branchpull	5	3	<i>Tree Play: Focal on Ground</i>
Jump	5	3	
Branchshake	5	3	
Bendsapling	5	3	
Climb	5	6	<i>Tree Play: Focal on Tree, No Contact</i>
Swing	5	6	
Fall	5	6	
Kick	11	6	<i>Tree Play: Focal on Tree, Contact</i>
Hang	11	6	
Shakeoff	11	6	
Stomp	7	5	<i>Initiation: Playful Approach</i>
Bop	7	5	
Bow	7	5	
Slapground	7	5	
Bite	6	4	
GrappleWrestle	6	4	<i>Contact Play: Wrestling</i>

Embrace	6	4	
Mount	6	4	
Pressdown	6	4	
Liedown	6	4	
Trip	6	4	
Moveother	6	4	
Headdown	6	4	
Hold	9	4	
Pull	9	4	
Touch	9	4	
Hit	9	4	<i>Contact Play: Moving</i>
Push	9	4	
Crouch	9	4	
DrumTree	3	2	
Flail	3	2	<i>Object Interaction: Drum Tree</i>
Armraise	3	2	
Rollobject	12	2	<i>Object Interaction: Initiation</i>
Pressground	12	2	
Carryobject	4	2	
Grabobject	4	2	<i>Object Interaction: Movement</i>
Armwave	4	2	
Swagger	4	2	
Exploreobject	10	7	<i>Object Interaction: Explore Object</i>
Hitobject	10	7	
Retreatbackwards	1	7	
Retreat	1	7	<i>Avoidance: Retreat</i>
Flee	2	7	
Armprotect	2	7	
Hide	2	7	<i>Avoidance: No Contact</i>
Feint	2	7	
Parry	9	7	
Circlepartner	9	7	<i>Avoidance: Contact</i>
Hideswing	3	7	<i>Avoidance: Transition to Tree</i>
Approach	1	1	
Bipedal	1	2	<i>Approach</i>
Armswing	1	2	
Circletree	8	1	
Lead	8	1	
Chase	8	1	<i>Follow: Chase</i>
Reach	8	1	
FollowOther	8	1	
Hitattempt	4	1	<i>Follow: Charge</i>
Charge	4	1	
Pirouette	9	1	<i>Follow: Pirouette</i>

Headshake	12	1	<i>Follow: Initiation</i>
Presentbodypart	12	-	<i>No Significant Transitions:</i>
Kickdirt	12	-	<i>Initiations</i>
Rock	4	-	<i>No Significant Transitions:</i>
Stareat	8	-	<i>Charge</i>
Jumpon	11	-	<i>No Significant Transitions:</i>
			<i>Focal on Tree</i>

499

500 **Discussion**

501 In this study, we explored the sequence structure of Western chimpanzee play behaviour
502 for the Bossou community. We were interested in how predictable play was, and whether
503 we find distinct ‘games’ with clear rules for sequences used by each player. Despite the
504 large number of play elements and of transitions that were observed infrequently, only a
505 small number of transitions occurred at higher-than-expected rates. Information about the
506 preceding play element allowed for more accurate predictions than random choice, and the
507 predictions became more accurate when including more antecedent elements – however,
508 play retained its unpredictability, as the accuracy of predictions remained low. The reason
509 for this can be found in the patterns of different ‘games’: we showed that there were
510 several clusters of highly connected play elements with similar transition patterns. Thus,
511 when a player was climbing in a tree, there were only few play elements available to them,
512 but the exact order cannot be predicted. This appears to be similar to human games – if two
513 children play tag, there is a finite number of play elements that each of them can use to
514 keep the game going, but it is not in either players interest to let the partner know which
515 one is next. Importantly, the clusters we detected indicated clear roles for at least some of
516 the games, with play partners on the ground acting different from the one in the tree and
517 avoiding play elements clearly distinguished from approaching elements in chases.

518 Animal play behaviour is characterised by its unpredictable nature compared to other
519 contexts, leading to theories that it has evolved as a method for young individuals to learn
520 social and motor skills that will become important later in life (Fagen, 1981; Smith, 1982).
521 We show that, at least for chimpanzees, play is a mix of predictability and unpredictability –
522 while knowledge of previous actions allows us to improve predictive accuracy, play
523 sequences are not simple Markov chains, where one or few antecedent actions allow for
524 accurate reactions. However, that does not mean that play is random, as clear games
525 emerged from our bottom-up, data driven approach. We detect clusters of elements that
526 are used together and interchangeably, indicating a rule-based system were the game limits
527 the number of appropriate responses. Further studies will have to determine whether non-
528 linear prediction methods, e.g., deep learning (Chollet & Allaire, 2018) could increase
529 predictive accuracy, and whether action sequences are better described using non-Markov
530 processes (Kershbaum et al., 2014). Using a naïve Bayes classifier strongly improved
531 predictive accuracy, and more complex machine learning algorithms and a larger dataset
532 could further extend our ability to detect transition patterns. For now, this study
533 demonstrates the power of a ‘grammar of actions’ approach (Pastra & Aloimonos, 2012),
534 where methods from natural language processing and syntactical analysis are employed to
535 understand the sequential nature of behavioural actions in humans and non-human
536 animals. Our study presents evidence that the ability of chimpanzees to produce
537 hierarchically structured sequences is not limited to their communication (Arcadi, 1996;
538 Girard-Buttoz et al., 2022; Liebal et al., 2004) and tool-related behaviour (Carvalho et al.,
539 2008; Estienne et al., 2017; Vale et al., 2017), but is also prevalent in fast-paced social
540 interactions that require adaptation to multiple partners in real time (McCarthy et al., 2013).

541 Some of the games have previously been identified by researcher when coding primate play
542 – for example, many studies code ‘rough-and-tumble’ play as an overarching category for all
543 physical play in close contact (Palagi et al., 2016). Our results show that this category can be
544 established with a data driven approach. The same is true for chasing games. Another
545 overarching context is tree-related play, either with the player climbing or on the ground.
546 Lastly, we identified social object play as its own context, which equally has attracted
547 research in the past as a possible window into game-like behaviour (Shimada, 2006; Tanner
548 & Byrne, 2010). Each of those games consisted of some central elements – holding the
549 partner, moving towards them, moving away from them, holding an object, hanging from a
550 tree etc. – that defined the context, with other elements added more freely, similar to tool
551 use sequences in chimpanzees (Carvalho et al., 2008). We found clear evidence of role-
552 reversal between players, as has long been described for play across species (Fagen, 1981) –
553 players on the ground have a clear role in tree play that differs from those of the partner in
554 the tree, and chasing players use different play elements than those fleeing. However, it
555 needs to be kept in mind that the small sample size for many of the elements makes some
556 of these clusters unreliable and dependent on researcher choices for the UMAP and
557 clustering algorithms.

558 The specific research context of this study, using video footage of the Bossou chimpanzees
559 while they are in the forest clearing of the outdoor lab, constrains the number of different
560 games that could be observed – for example, water games as in mountain gorillas (Costa et
561 al., 2019) cannot be observed in this environment. The physical substrate around the
562 outdoor lab limits the amount of arboreal play. Thus, while we describe a method to detect
563 games, larger datasets and more varied collection contexts would be necessary to
564 characterise chimpanzee games more broadly. We are not trying to describe species-specific

565 play patterns for chimpanzees in general (which probably include strong developmental,
566 individual, dyadic, and group-level effects), but show that in this fairly standardised sample,
567 chimpanzee play shows complex sequential patterns. Importantly, our approach would
568 allow direct comparisons between different communities of chimpanzees, based on
569 transition probabilities and network patterns. As the form of play is less defined by its
570 function than for example tool use, this might be a useful approach to study cultural
571 differences in a meaningful way (Boesch et al., 2020).

572 One aspect currently missing from the picture is partner behaviour: while within-player
573 behaviour shows limited predictability, it might be more predictable when knowing what
574 the partner did. Chimpanzees and other primates engage in turn-taking when
575 communicating (Chow et al., 2015; Fröhlich, 2017), and play has been described as a context
576 that elicits joint commitment between players, with clear evidence that they re-establish
577 that commitment after breaks (Heesen, Bangerter, et al., 2021; Heesen, Zuberbühler, et al.,
578 2021). Thus, we need an approach that understands social interactions (including play) as a
579 complex system of decisions taken by all involved individuals. One question is whether play
580 is indeed more complex in its sequential structure than other social contexts, such as
581 grooming or aggressions, or communicative exchanges. The statistical analyses underlying
582 this study can be replicated using any data consisting of sequences of discrete elements.

583 The data collection, pre-processing, and analytical choices of this study introduce several
584 researcher degrees of freedom that limit generalisability of results (Wicherts et al., 2016).
585 Thus, we are interpreting all results regarding the structure of play element transitions
586 conditional on the coding scheme and group. The Bossou chimpanzees are a very small
587 group and subadult players lack same-aged play partners. Results were based on a small

588 number of players who had an outsized impact on the dataset, and accounting for
589 individual-level idiosyncrasies and age-dependent contingencies in transitions between play
590 elements might dramatically improve predictability (Cordoni & Palagi, 2011). Many play
591 elements were rare, and we had to make choices on how to combine them; there was still
592 considerably uncertainty for some of the transition probability estimates. We set strict cut-
593 offs for significance levels and the minimum number of observed transitions to err
594 conservatively, but an increased dataset or different thresholds might influence results.
595 Another choice we had to make was regarding co-occurring play elements. We chose to use
596 permutations to randomly assign which elements occurred at what point in the sequence,
597 but this approach necessarily increases noise in the data. Lastly, every study of play
598 behaviour is using a different ethogram, with different levels of complexity. We would
599 predict that a simpler coding scheme would result in higher predictability. Because of the
600 complexity of the coding scheme chosen here, no inter-rater reliability was performed, thus
601 results should be interpreted as conditional on the coding process.

602 In summary, we show that chimpanzee play behaviour is a complex sequential process with
603 an identifiable hierarchical structure – chimpanzees play games consisting of play elements
604 that are interchangeable in their sequence position and transition into each other at higher
605 rates than they transition into play elements that are representative of other games.
606 Information about previous actions allows for prediction of subsequent elements and
607 including more antecedent elements improves accuracy. Our results show that there is
608 considerable leeway to study decision-making and cognitive complexity in animal social
609 interactions on the micro-level (Gygax et al., 2021), but this process, like the study of
610 communication, requires detailed video analysis of long-term data (Hobaiter & Byrne,
611 2011). In the future, being able to achieve reliable behaviour recognition from video

612 databases, as has been demonstrated for the Bossou chimpanzees (Bain et al., 2021), could
613 be a valuable tool in reducing the coding effort involved. As it stands, our results further
614 highlight the special place play behaviour holds in the cognitive and behavioural
615 development of chimpanzees – by creating a safe environment to explore and train fast-
616 paced behavioural sequences, it allows young individuals to learn to predict how a partner
617 will react in different social situations.

618

619 **Data Availability:** All data and R scripts are available in a bespoke GitHub repository that
620 allows reproduction and replication (<https://github.com/AlexMielke1988/Mielke->
621 [Carvalho_Chimpanzee-Play](#)).

622 **Acknowledgements:** This research was funded by the British Academy through AM's
623 Newton International Fellowship. AM also received funding from the Leverhulme Trust. We
624 thank Professor Tetsuro Matsuzawa for the long-term efforts to develop and support the
625 research on wild chimpanzees, at the Bossou Field Station, in Guinea. Those efforts were
626 supported by grants from MEXT (#12002009, #16002001, #20002001, #24000001,
627 #16H06283) and JSPS (Core-to-core CCSN and U04-PWS). We thank Daniel Schofield and
628 Misato Hayashi for their continuous help in curating the Bossou video archive, and Sophie
629 Berdugo for help identifying the chimpanzees. We are also very grateful to Dora Biro,
630 Catherine Hobaiter, David R. Braun, and all the KUPRI researchers who helped to collect
631 field data at Bossou between 2009 and 2013. Special thanks are due to Direction General de
632 la Recherche Scientifique et l'innovation Technologique (DGERSIT) and to Dr. Ali Gaspard
633 Soumah and the Institut de Recherche Environnementale de Bossou (IREB), République de
634 Guinée, for assistance and research permission to conduct field work at Bossou; as well as
635 research assistants Boniface Zogbila, Gouanou Zogbila, Henry Didier Camara, and Gilles
636 Doré, Pascal Goumy, for their invaluable assistance in the field.

637

638 **Competing interests:** The authors declare that they have no competing interests.

639

640 **References**

- 641 Allen, J. A., Garland, E. C., Dunlop, R. A., & Noad, M. J. (2019). Network analysis reveals
642 underlying syntactic features in a vocally learnt mammalian display, humpback whale
643 song. *Proceedings of the Royal Society B: Biological Sciences*, 286(1917).
644 <https://doi.org/10.1098/rspb.2019.2014>
- 645 Arcadi, A. C. (1996). Phrase structure of wild chimpanzee pant hoots: Patterns of production
646 and interpopulation variability. *American Journal of Primatology*, 39(3), 159–178.
- 647 Arnold, K., & Zuberbühler, K. (2008). Meaningful call combinations in a non-human primate.
648 *Current Biology*, 18(5), R202–R203. <https://doi.org/10.1016/J.CUB.2008.01.040>
- 649 Aychet, J., Blois-Heulin, C., & Lemasson, A. (2021). Sequential and network analyses to
650 describe multiple signal use in captive mangabeys. *Animal Behaviour*, 182, 203–226.
651 <https://doi.org/10.1016/J.ANBEHAV.2021.09.005>
- 652 Bain, M., Nagrani, A., Schofield, D., Berdugo, S., Bessa, J., Owen, J., Hockings, K. J.,
653 Matsuzawa, T., Hayashi, M., Biro, D., Carvalho, S., & Zisserman, A. (2021). Automated
654 audiovisual behavior recognition in wild primates. *Science Advances*, 7(46), 4883.
655 <https://doi.org/10.1126/SCIADV.ABI4883>
- 656 Barceló-Coblijn, L., Serna Salazar, D., Isaza, G., Castillo Ossa, L. F., & Bedia, M. G. (2017).
657 Netlang: A software for the linguistic analysis of corpora by means of complex
658 networks. *PLoS ONE*, 12(8), e0181341. <https://doi.org/10.1371/journal.pone.0181341>
- 659 Bard, K. A., Dunbar, S., Maguire-Herring, V., Veira, Y., Hayes, K. G., & McDonald, K. (2014).
660 Gestures and social-emotional communicative development in chimpanzee infants.
661 *American Journal of Primatology*, 76(1), 14–29. <https://doi.org/10.1002/AJP.22189>

- 662 Bekoff, M., & Allen, C. (1998). Intentional communication and social play: how and why
663 animals negotiate and agree to play. In *Animal Play* (pp. 97–114). Cambridge University
664 Press. <https://doi.org/10.1017/CBO9780511608575.006>
- 665 Berwick, R. C., Okanoya, K., Beckers, G. J. L., & Bolhuis, J. J. (2011). Songs to syntax: the
666 linguistics of birdsong. *Trends in Cognitive Sciences*, *15*(3), 113–121.
667 <https://doi.org/10.1016/j.tics.2011.01.002>
- 668 Boesch, C., Kalan, A. K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, E. A.,
669 Barciela, A., Coupland, C., Egbe, V. E., Eno-Nku, M., Michael Fay, J., Fine, D., Adriana
670 Hernandez-Aguilar, R., Hermans, V., Kadam, P., Kambi, M., Llana, M., Maretti, G., ...
671 Kühl, H. S. (2020). Chimpanzee ethnography reveals unexpected cultural diversity.
672 *Nature Human Behaviour* *2020 4:9*, *4*(9), 910–916. [https://doi.org/10.1038/s41562-](https://doi.org/10.1038/s41562-020-0890-1)
673 [020-0890-1](https://doi.org/10.1038/s41562-020-0890-1)
- 674 Bohn, K. M., Schmidt-French, B., Schwartz, C., Smotherman, M., & Pollak, G. D. (2009).
675 Versatility and Stereotypy of Free-Tailed Bat Songs. *PLOS ONE*, *4*(8), e6746.
676 <https://doi.org/10.1371/JOURNAL.PONE.0006746>
- 677 Bosshard, A. B., Leroux, M., Lester, N. A., Bickel, B., Stoll, S., & Townsend, S. W. (2021). From
678 collocations to call-ocations: using linguistic methods to quantify animal call
679 combinations. *BioRxiv*.
- 680 Bshary, R., & Oliveira, R. F. (2015). Cooperation in animals: toward a game theory within the
681 framework of social competence. *Current Opinion in Behavioral Sciences*, *3*, 31–37.
682 <https://doi.org/10.1016/J.COBEHA.2015.01.008>

- 683 Burghardt, G. M. (2015). Play in fishes, frogs and reptiles. *Current Biology*, 25(1), R9–R10.
684 <https://doi.org/10.1016/j.cub.2014.10.027>
- 685 Carvalho, S., Cunha, E., Sousa, C., & Matsuzawa, T. (2008). Chaînes opératoires and
686 resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal*
687 *of Human Evolution*, 55(1), 148–163. <https://doi.org/10.1016/J.JHEVOL.2008.02.005>
- 688 Chollet, F., & Allaire, J. J. (2018). Deep Learning in R. In *R-bloggers* (Issue 7080). Manning
689 Publications. <https://www.manning.com/books/deep-learning-with-r>
- 690 Chow, C. P., Mitchell, J. F., & Miller, C. T. (2015). Vocal turn-taking in a non-human primate is
691 learned during ontogeny. *Proceedings of the Royal Society B: Biological Sciences*,
692 282(1807), 20150069. <https://doi.org/10.1098/rspb.2015.0069>
- 693 Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The Syntax and Meaning of Wild Gibbon
694 Songs. *PLOS ONE*, 1(1), e73. <https://doi.org/10.1371/JOURNAL.PONE.0000073>
- 695 Cordoni, G., Norscia, I., Bobbio, M., & Palagi, E. (2018). differences in play can illuminate
696 differences in affiliation a comparative study on chimpanzees and gorillas. *PLOS ONE*.
697 <https://doi.org/10.1371/journal.pone.0193096>
- 698 Cordoni, G., & Palagi, E. (2011). Ontogenetic trajectories of chimpanzee social play:
699 Similarities with humans. *PLOS ONE*, 6(11).
700 <https://doi.org/10.1371/journal.pone.0027344>
- 701 Cordoni, G., & Palagi, E. (2012). Fair play and honest signals in immature chimpanzees. *Atti*
702 *Della Societa Toscana Di Scienze Naturali, Memorie Serie B*, 119, 97–101.
703 <https://doi.org/10.2424/ASTSN.M.2012.14>

- 704 Costa, R. F. P., Hayashi, M., Huffman, M. A., Kalema-Zikusoka, G., & Tomonaga, M. (2019).
705 Water games by mountain gorillas: implications for behavioral development and
706 flexibility—a case report. *Primates*, 60(6), 493–498. [https://doi.org/10.1007/s10329-](https://doi.org/10.1007/s10329-019-00749-6)
707 019-00749-6
- 708 Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research.
709 In *InterJournal Complex Systems: Vol. Complex Sy* (Issue 1695). <http://igraph.sf.net>
- 710 Davila Ross, M., J Owren, M., Zimmermann, E., Ross, M. D., Owren, M. J., & Zimmermann, E.
711 (2009). Reconstructing the Evolution of Laughter in Great Apes and Humans. *Current*
712 *Biology*, 19(13), 1106–1111. <https://doi.org/10.1016/j.cub.2009.05.028>
- 713 Davila-Ross, M., Allcock, B., Thomas, C., & Bard, K. A. (2011). Aping expressions?
714 Chimpanzees produce distinct laugh types when responding to laughter of others.
715 *Emotion*, 11(5), 1013–1020. <https://doi.org/10.1037/a0022594>
- 716 Deblauwe, I., Guislain, P., Dupain, J., & van Elsacker, L. (2006). Use of a tool-set by Pan
717 troglodytes troglodytes to obtain termites (Macrotermes) in the periphery of the Dja
718 Biosphere Reserve, southeast Cameroon. *American Journal of Primatology*, 68(12),
719 1191–1196. <https://doi.org/10.1002/AJP.20318>
- 720 Demartsev, V., Strandburg-Peshkin, A., Ruffner, M., & Manser, M. (2018). Vocal Turn-Taking
721 in Meerkat Group Calling Sessions. *Current Biology*, 28(22), 3661-3666.e3.
722 <https://doi.org/10.1016/j.cub.2018.09.065>
- 723 Diamond, J., & Bond, A. B. (2003). A comparative analysis of social play in birds. *Behaviour*.
724 <https://doi.org/10.1163/156853903322589650>

- 725 Eisenstein, J. (2019). *Introduction to Natural Language Processing. Adaptive Computation*
726 *and Machine Learning serie*. 536. <https://mitpress.mit.edu/books/introduction-natural->
727 [language-processing](https://mitpress.mit.edu/books/introduction-natural-language-processing)
- 728 Engesser, S., Ridley, A. R., & Townsend, S. W. (2016). Meaningful call combinations and
729 compositional processing in the southern pied babbler. *Proceedings of the National*
730 *Academy of Sciences of the United States of America*, 113(21), 5976–5981.
731 <https://doi.org/10.1073/PNAS.1600970113/-/DCSUPPLEMENTAL>
- 732 Estienne, V., Stephens, C., & Boesch, C. (2017). Extraction of honey from underground bee
733 nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National
734 Park, Gabon: Techniques and individual differences. *American Journal of Primatology*,
735 79(8), e22672. <https://doi.org/10.1002/AJP.22672>
- 736 Fagen, R. M. (1981). *Animal Play Behavior*. Oxford University Press.
- 737 Fernandez-Duque, E., Valeggia, C. R., Mason, W. A., Pellis, S. M., & Iwaniuk, A. N. (2000).
738 Adult-adult play in primates: Comparative analyses of its origin, distribution and
739 evolution. *Ethology*, 106(12), 1083–1104. <https://doi.org/10.1046/j.1439->
740 [0310.2000.00627.x](https://doi.org/10.1046/j.1439-0310.2000.00627.x)
- 741 Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software
742 for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11),
743 1325–1330. <https://doi.org/10.1111/2041-210X.12584>
- 744 Fröhlich, M. (2017). Taking turns across channels: Conversation-analytic tools in animal
745 communication. *Neuroscience & Biobehavioral Reviews*, 80, 201–209.
746 <https://doi.org/10.1016/j.neubiorev.2017.05.005>

- 747 Fröhlich, M., Wittig, R. M., & Pika, S. (2016). Play-solicitation gestures in chimpanzees in the
748 wild: Flexible adjustment to social circumstances and individual matrices. *Royal Society*
749 *Open Science*, 3(8), e160278. <https://doi.org/10.1098/rsos.160278>
- 750 Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of the
751 gorilla (*Gorilla gorilla*): Repertoire, intentionality and possible origins. *Animal Cognition*,
752 12(3), 527–546. <https://doi.org/10.1007/s10071-009-0213-4>
- 753 Genty, E., & Byrne, R. W. (2010). Why do gorillas make sequences of gestures? *Animal*
754 *Cognition*, 13(2), 287–301. <https://doi.org/10.1007/s10071-009-0266-4>
- 755 Girard-Buttoz, C., Zaccarella, E., Bortolato, T., Friederici, A. D., Wittig, R. M., & Crockford, C.
756 (2022). Chimpanzees produce diverse vocal sequences with ordered and
757 recombinatorial properties. *Communications Biology*, 5(1).
758 <https://doi.org/10.1038/S42003-022-03350-8>
- 759 Graham, K. E., Furuichi, T., & Byrne, R. W. (2017). The gestural repertoire of the wild bonobo
760 (*Pan paniscus*): a mutually understood communication system. *Animal Cognition*, 20(2),
761 171–177. <https://doi.org/10.1007/s10071-016-1035-9>
- 762 Graham, K. E., Furuichi, T., & Byrne, R. W. (2020). Context, not sequence order, affects the
763 meaning of bonobo (*Pan paniscus*) gestures. *Gesture*, 19(2–3), 335–364.
764 <https://doi.org/10.1075/GEST.19028.GRA/CITE/REFWORKS>
- 765 Gygax, L., Zeeland, Y. R. A., Rufener, | Christina, & Daniel, A. (2021). Fully flexible analysis of
766 behavioural sequences based on parametric survival models with frailties—A tutorial.
767 *Ethology*, 00, 1–14. <https://doi.org/10.1111/ETH.13225>

- 768 Heesen, R., Bangerter, A., Zuberbühler, K., Iglesias, K., Neumann, C., Pajot, A., Perrenoud, L.,
769 Guéry, J.-P., Rossano, F., & Genty, E. (2021). Assessing joint commitment as a process in
770 great apes. *iScience*, 24(8), 102872. <https://doi.org/10.1016/J.ISCI.2021.102872>
- 771 Heesen, R., Genty, E., Rossano, F., Zuberbühler, K., & Bangerter, A. (2017). Social play as
772 joint action: A framework to study the evolution of shared intentionality as an
773 interactional achievement. *Learning & Behavior*, 45(4), 390–405.
774 <https://doi.org/10.3758/s13420-017-0287-9>
- 775 Heesen, R., Zuberbühler, K., Bangerter, A., Iglesias, K., Rossano, F., Pajot, A., Guéry, J.-P., &
776 Genty, E. (2021). Evidence of joint commitment in great apes' natural joint actions.
777 *Royal Society Open Science*, 8(12). <https://doi.org/10.1098/RSOS.211121>
- 778 Hihara, S., Obayashi, S., Tanaka, M., & Iriki, A. (2003). Rapid learning of sequential tool use
779 by macaque monkeys. *Physiology & Behavior*, 78.
- 780 Hobaiter, C., & Byrne, R. W. (2011). The gestural repertoire of the wild chimpanzee. *Animal*
781 *Cognition*, 14(5), 745–767. <https://doi.org/10.1007/s10071-011-0409-2>
- 782 Hobaiter, C., & Byrne, R. W. (2014). The meanings of chimpanzee gestures. *Current Biology*,
783 24(14), 1596–1600. <https://doi.org/10.1016/j.cub.2014.05.066>
- 784 Hunt, G., & Gray, R. (2004). The crafting of hook tools by wild New Caledonian crows.
785 *Proceedings of the Royal Society of London B*.
- 786 Kershenbaum, A., Blumstein, D. T., Roch, M. A., Akçay, Ç., Backus, G., Bee, M. A., Bohn, K.,
787 Cao, Y., Carter, G., Cäsar, C., Coen, M., DeRuiter, S. L., Doyle, L., Edelman, S., Ferrer-i-
788 Cancho, R., Freeberg, T. M., Garland, E. C., Gustison, M., Harley, H. E., ... Zamora-

- 789 Gutierrez, V. (2016). Acoustic sequences in non-human animals: a tutorial review and
790 prospectus. *Biological Reviews*, 91(1), 13–52. <https://doi.org/10.1111/brv.12160>
- 791 Kershenbaum, A., Bowles, A. E., Freeberg, T. M., Jin, D. Z., Lameira, A. R., & Bohn, K. (2014).
792 Animal vocal sequences: Not the Markov chains we thought they were. *Proceedings of*
793 *the Royal Society B: Biological Sciences*, 281(1792).
794 <https://doi.org/10.1098/rspb.2014.1370>
- 795 Kershenbaum, A., Ilany, A., Blaustein, L., & Geffen, E. (2012). Syntactic structure and
796 geographical dialects in the songs of male rock hyraxes. *Proceedings of the Royal*
797 *Society B: Biological Sciences*, 279(1740), 2974–2981.
798 <https://doi.org/10.1098/RSPB.2012.0322>
- 799 Konopka, T. (2022). *umap: Uniform Manifold Approximation and Projection (0.2.8.0)*.
- 800 Koops, K., Furuichi, T., & Hashimoto, C. (2015). Chimpanzees and bonobos differ in intrinsic
801 motivation for tool use. *Scientific Reports 2015 5:1*, 5(1), 1–7.
802 <https://doi.org/10.1038/srep11356>
- 803 Kuba, M. J., Byrne, R. A., Meisel, D. v., & Mather, J. A. (2006). When do octopuses play?
804 Effects of repeated testing, object type, age, and food deprivation on object play in
805 *Octopus vulgaris*. *Journal of Comparative Psychology*, 120(3), 184–190.
806 <https://doi.org/10.1037/0735-7036.120.3.184>
- 807 Leisterer-Peoples, S. M., Ross, C. T., Greenhill, S. J., Hardecker, S., & Haun, D. B. M. (2021).
808 Games and enculturation: A cross-cultural analysis of cooperative goal structures in
809 Austronesian games. *PLOS ONE*, 16(11), e0259746.
810 <https://doi.org/10.1371/journal.pone.0259746>

- 811 Leroux, M., Bosshard, A. B., Chandia, B., Manser, A., Zuberbühler, K., & Townsend, S. W.
812 (2021). Chimpanzees combine pant hoots with food calls into larger structures. *Animal*
813 *Behaviour*, 179, 41–50. <https://doi.org/10.1016/J.ANBEHAV.2021.06.026>
- 814 Levshina, N. (2015). *How To Do Linguistics with R*. John Benjamins Publishing Company.
- 815 Liebal, K., Call, J., & Tomasello, M. (2004). Use of gesture sequences in chimpanzees.
816 *American Journal of Primatology*, 64(4), 377–396. <https://doi.org/10.1002/ajp.20087>
- 817 Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. (2022). *cluster: Cluster*
818 *Analysis Basics and Extensions* (2.1.3).
- 819 Martin-Ordas, G., Schumacher, L., & Call, J. (2012). Sequential Tool Use in Great Apes. *PLOS*
820 *ONE*, 7(12), e52074. <https://doi.org/10.1371/JOURNAL.PONE.0052074>
- 821 Matsusaka, T. (2004). When does play panting occur during social play in wild chimpanzees?
822 *Primates*, 45(4), 221–229. <https://doi.org/10.1007/s10329-004-0090-z>
- 823 Matsuzawa, T. (2020). Pretense in chimpanzees. *Primates*, 61(4), 543–555.
824 <https://doi.org/10.1007/S10329-020-00836-Z/FIGURES/5>
- 825 Matsuzawa, T., & Humle, T. (2011). Bossou: 33 Years. In *The chimpanzees of Bossou and*
826 *Nimba*. (pp. 3–10). https://doi.org/10.1007/978-4-431-53921-6_2
- 827 McCarthy, M. S., Jensvold, M. L. A., & Fouts, D. H. (2013). Use of gesture sequences in
828 captive chimpanzee (*Pan troglodytes*) play. *Animal Cognition*, 16(3), 471–481.
829 <https://doi.org/10.1007/s10071-012-0587-6>
- 830 McInnes, L., Healy, J., & Melville, J. (2020). *UMAP: Uniform Manifold Approximation and*
831 *Projection for Dimension Reduction*. <https://onikle.com/articles/284481>

- 832 Meyer, D., Dimitriadou, E., Hornik, K., Weingessel, A., & Leisch, F. (2021). *e1071: Misc*
833 *Functions of the Department of Statistics, Probability Theory Group* (1.7-9). TU Wien.
- 834 Mielke, A., Waller, B. M., Pérez, C., Rincon, A. v., Duboscq, J., & Micheletta, J. (2021).
835 NetFACS: Using network science to understand facial communication systems. *Behavior*
836 *Research Methods 2021*, 1–16. <https://doi.org/10.3758/S13428-021-01692-5>
- 837 Myowa-Yamakoshi, M., & Yamakoshi, G. (2011). Play Behaviors Involving the Use of Objects
838 in Young Chimpanzees at Bossou. In *The Chimpanzees of Bossou and Nimba* (pp. 231–
839 240). Springer, Tokyo. https://doi.org/10.1007/978-4-431-53921-6_25
- 840 Nakamura, M. (2012). Playing with His Leg: A Case of Imaginary Social Play by an Adolescent
841 Male Chimpanzee at Bossou? *Pan Africa News*, 19(1), 1–3.
- 842 Newman, M. (2010). Networks: An Introduction. In *Networks: An Introduction*. Oxford
843 University Press. <https://doi.org/10.1093/acprof:oso/9780199206650.001.0001>
- 844 Nishida, T., Zamma, K., Matsusaka, T., Inaba, A., & McGrew, W. C. (2010). Chimpanzee
845 Behavior in the Wild. In *Chimpanzee Behavior in the Wild*. Springer Science & Business
846 Media. <https://doi.org/10.1007/978-4-431-53895-0>
- 847 Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's monkeys concatenate
848 vocalizations into context-specific call sequences. *Proceedings of the National Academy*
849 *of Sciences*, 106(51), 22026–22031. <https://doi.org/10.1073/PNAS.0908118106>
- 850 Palagi, E., Burghardt, G. M., Smuts, B., Cordoni, G., Dall'Olio, S., Fouts, H. N., Řeháková-
851 Petrů, M., Siviý, S. M., & Pellis, S. M. (2016). Rough-and-tumble play as a window on
852 animal communication. *Biological Reviews*, 91(2), 311–327.
853 <https://doi.org/10.1111/brv.12172>

- 854 Palagi, E., Cordoni, G., Borgognini Tarli, S. M., Tarli, S. M. B., & Borgognini Tarli, S. M. (2004).
855 Immediate and delayed benefits of play behaviour: New evidence from Chimpanzees
856 (Pan troglodytes). *Ethology*, *110*(12), 949–962. <https://doi.org/10.1111/j.1439->
857 [0310.2004.01035.x](https://doi.org/10.1111/j.1439-0310.2004.01035.x)
- 858 Pastra, K., & Aloimonos, Y. (2012). The minimalist grammar of action. *Philosophical*
859 *Transactions of the Royal Society B: Biological Sciences*, *367*(1585), 103–117.
860 <https://doi.org/10.1098/rstb.2011.0123>
- 861 Pedersen, T. L. (2021). *ggraph: An Implementation of Grammar of Graphics for Graphs and*
862 *Networks* (R package version 2.0.5.).
- 863 Petrů, M., M, S., Charvátová, Lhota, S., Špinka, M., Charvátová, V., & Lhota, S. (2009).
864 Revisiting Play Elements and Self-Handicapping in Play: A Comparative Ethogram of
865 Five Old World Monkey Species. *Journal of Comparative Psychology*, *123*(3), 250–263.
866 <https://doi.org/10.1037/a0016217>
- 867 Pika, S., & Zuberbühler, K. (2008). Social games between bonobos and humans: Evidence for
868 shared intentionality? *American Journal of Primatology*, *70*(3), 207–210.
869 <https://doi.org/10.1002/ajp.20469>
- 870 R Development Core Team, & R Core Team. (2020). R: A language and environment for
871 statistical computing. *R Foundation for Statistical Computing Vienna Austria, 0*, {ISBN}
872 [3-900051-07-0. https://doi.org/10.1038/sj.hdy.6800737](https://doi.org/10.1038/sj.hdy.6800737)
- 873 Ross, K. M., Bard, K. A., & Matsuzawa, T. (2014). Playful expressions of one-year-old
874 chimpanzee infants in social and solitary play contexts. *Frontiers in Psychology*, *5*.
875 <https://doi.org/10.3389/fpsyg.2014.00741>

- 876 Rousseeuw, P. J. (1987). Silhouettes: A graphical aid to the interpretation and validation of
877 cluster analysis. *Journal of Computational and Applied Mathematics*, 20(C), 53–65.
878 [https://doi.org/10.1016/0377-0427\(87\)90125-7](https://doi.org/10.1016/0377-0427(87)90125-7)
- 879 Safryghin, A., Cross, C., Fallon, B., Heesen, R., Ferrer-I, R., 2&, C., & Hobaiter, C. (2021).
880 Linguistic laws are not the law in chimpanzee sexual solicitation gestures. *BioRxiv*,
881 2021.05.19.444810. <https://doi.org/10.1101/2021.05.19.444810>
- 882 Sasahara, K., Cody, M. L., Cohen, D., & Taylor, C. E. (2012). Structural Design Principles of
883 Complex Bird Songs: A Network-Based Approach. *PLoS ONE*, 7(9), e44436.
884 <https://doi.org/10.1371/journal.pone.0044436>
- 885 Shimada, M. (2006). Social object play among young japanese macaques (*macaca fuscata*) in
886 Arashiyama, Japan. *Primates*, 47(4), 342–349. [https://doi.org/10.1007/s10329-006-](https://doi.org/10.1007/s10329-006-0187-7)
887 0187-7
- 888 Shimada, M. (2013). Dynamics of the temporal structures of playing clusters and cliques
889 among wild chimpanzees in Mahale Mountains National Park. *Primates*, 54(3), 245–
890 257. <https://doi.org/10.1007/s10329-013-0348-4>
- 891 Silge, J., & Robinson, D. (2017). *Text Mining with R*. <https://www.tidytextmining.com/>
- 892 Sirianni, G., Mundry, R., & Boesch, C. (2015). When to choose which tool: multidimensional
893 and conditional selection of nut-cracking hammers in wild chimpanzees. *Animal*
894 *Behaviour*, 100, 152–165. <https://doi.org/10.1016/J.ANBEHAV.2014.11.022>
- 895 Smith, P. K. (1982). Does play matter? Functional and evolutionary aspects of animal and
896 human play. *Behavioral and Brain Sciences*, 5(1), 139–155.
897 <https://doi.org/10.1017/S0140525X0001092X>

- 898 Sonnweber, R., Ravignani, A., & Fitch, W. T. (2015). Non-adjacent visual dependency
899 learning in chimpanzees. *Animal Cognition*, *18*(3), 733–745.
900 <https://doi.org/10.1007/s10071-015-0840-x>
- 901 Tanner, J. E., & Byrne, R. W. (2010). Triadic and collaborative play by gorillas in social games
902 with objects. *Animal Cognition*, *13*(4), 591–607. [https://doi.org/10.1007/s10071-009-](https://doi.org/10.1007/s10071-009-0308-y)
903 [0308-y](https://doi.org/10.1007/s10071-009-0308-y)
- 904 ten Cate, C. (2014). On the phonetic and syntactic processing abilities of birds: From songs
905 to speech and artificial grammars. *Current Opinion in Neurobiology*, *28*, 157–164.
906 <https://doi.org/10.1016/j.conb.2014.07.019>
- 907 Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and
908 sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*,
909 *28*(5), 675–691. <https://doi.org/10.1017/S0140525X05000129>
- 910 Vale, G. L., Davis, S. J., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2017). Acquisition of a
911 socially learned tool use sequence in chimpanzees: Implications for cumulative culture.
912 *Evolution and Human Behavior*, *38*(5), 635–644.
913 <https://doi.org/10.1016/J.EVOLHUMBEHAV.2017.04.007>
- 914 Waller, B. M., & Cherry, L. (2012). Facilitating Play Through Communication: Significance of
915 Teeth Exposure in the Gorilla Play Face. *American Journal of Primatology*, *74*(2), 157–
916 164. <https://doi.org/10.1002/ajp.21018>
- 917 Waller, B. M., & Dunbar, R. I. M. (2005). Differential behavioural effects of silent bared teeth
918 display and relaxed open mouth display in chimpanzees (*Pan troglodytes*). *Ethology*,
919 *111*(2), 129–142. <https://doi.org/10.1111/j.1439-0310.2004.01045.x>

- 920 Weiss, M., Hultsch, H., Adam, I., Scharff, C., & Kipper, S. (2014). The use of network analysis
921 to study complex animal communication systems: A study on nightingale song.
922 *Proceedings of the Royal Society B: Biological Sciences*, 281(1785).
923 <https://doi.org/10.1098/rspb.2014.0460>
- 924 Wicherts, J. M., Veldkamp, C. L. S., Augusteijn, H. E. M., Bakker, M., van Aert, R. C. M., & van
925 Assen, M. A. L. M. (2016). Degrees of Freedom in Planning, Running, Analyzing, and
926 Reporting Psychological Studies: A Checklist to Avoid p-Hacking. *Frontiers in*
927 *Psychology*, 7, 1832. <https://doi.org/10.3389/fpsyg.2016.01832>
- 928 Wimpenny, J. H., Weir, A. A. S., Clayton, L., Rutz, C., & Kacelnik, A. (2009). Cognitive
929 Processes Associated with Sequential Tool Use in New Caledonian Crows. *PLOS ONE*,
930 4(8), e6471. <https://doi.org/10.1371/JOURNAL.PONE.0006471>
- 931 Zuberbühler, K. (2019). Evolutionary roads to syntax. *Animal Behaviour*, 151, 259–265.
932 <https://doi.org/10.1016/J.ANBEHAV.2019.03.006>
- 933
- 934