

1 **Wild-captive contrasts in non-vocal communicative repertoires and functional specificity in**
2 **orang-utans**

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13

14 **Abstract**

15 The creation of novel communicative acts is an essential element of human language. Although some
16 research suggests the presence of this ability in great apes, this claim remains controversial. Here, we
17 use orang-utans (*Pongo* spp.) to systematically assess the effect of the wild-captive contrast on the
18 repertoire size of communicative acts. We find that individual communicative repertoires are
19 significantly larger in captive compared to wild settings, irrespective of species, age-sex class or
20 sampling effort. Twenty percent of the orang-utan repertoire in captivity were not observed in the
21 wild. In Sumatran orang-utans, the more sociable species, functional specificity was also higher in
22 captive versus wild settings. We thus conclude that orang-utans, when exposed to a more sociable

23 and terrestrial lifestyle, have the behavioural plasticity to invent new communicative behaviours that
24 are highly functionally specific. This productive capacity by great apes is a major prerequisite for the
25 evolution of language and seems to be ancestral in the hominid lineage.

26

27 **Keywords**

28 Close-range communication, gesture, signal repertoire, signal meaning, behavioural plasticity, socio-
29 ecological environment, language evolution, *Pongo abelii*, *Pongo pygmaeus*

30

31 **Introduction**

32 One of the core features of human language is its productivity, referring to the idea that signallers
33 can create and understand novel utterances with novel meanings¹. While several other building
34 blocks of language, including intentionality, reference and compositional syntax, have increasingly
35 been documented among a wide range of non-human species^{2,3,4}, productivity seems to be very rare
36 in the animal kingdom. Instead, animal communication systems are thought to rely heavily on
37 evolved signals, that is, communicative acts whose form and function evolved under the influence of
38 the effect on the recipient^{5,6}. The current consensus is that all facial, vocal and most gestural
39 expressions of non-human species have evolved through natural selection over long periods of time,
40 and have become innate: the ability to produce them arises spontaneously during ontogeny, whereas
41 its use is often fine-tuned by practice^{7,8,9}.

42

43 Recent research on great apes, our closest living relatives, suggests that it may be timely to
44 distinguish between innate animal signals and those that are acquired developmentally¹⁰. Great apes
45 have provided most comparative evidence for the cognitive building blocks and selective pressures

46 shaping the human communication system^{11, 12, 13}. But recent work has also shown that some of their
47 gestures and sounds are apparently innovated and maintained over time^{14, 15, 16, 17, 18, 19, 20}, and play
48 the same role in the communication process as evolved signals do – we could thus call them invented
49 signals. Because targeted studies to estimate the extent of productivity in great apes are so far
50 lacking, we here examine this question by comparing the same species in the wild and in a novel
51 setting, captivity^{10, 21}. The contrast allows a direct test of how repertoires respond to the changes in
52 the socio-ecological environment. In captivity, individuals face less competition for food, have more
53 spare time, are closer together, are more often visible to each other, and more on the ground than in
54 the wild^{22, 23}. Especially in fission-fusion species such as orang-utans (*Pongo* spp.), interaction rates
55 in contexts such as social play, grooming, conflict situations and mating are boosted in captive
56 settings e.g.^{24, 25, 26}, which may favour the production of innovative communicative acts, and thus
57 cause differences in the communicative repertoires of individuals and groups.

58

59 The captive-wild contrast also allows us to examine the extent to which the meaning of
60 communicative acts depends on the context in which they are used. We predict that the learned,
61 “species-atypical” communicative acts have high functional specificity, i.e. a highly context-specific
62 production^{10, 27, 28}, a phenomenon reflecting communicative plasticity. This is because the use of
63 invented signals inevitably implies intentionality: naïve individuals observed and learned them,
64 inferred their meaning from context and reactions, and subsequently used them in the same context
65 with the same function as their original inventor but see^{29, 30} for contrary views on highly conserved signal production.
66 In contrast, evolved signals may be used intentionally or non-intentionally. They may therefore vary
67 in functional specificity, and show more communicative flexibility: the same communicative act
68 serves several different goals or functions, relying on context to provide disambiguation^{2, 31}.

69

70 The aim of the present study was to examine repertoires and functional specificity of close-range
71 communicative acts, in both wild and captive populations of orang-utans, the great ape genus which
72 is in our view ideal for this avenue of research. Systematic studies on the gestural repertoire of
73 captive orang-utans have demonstrated that their propensity for elaborate and flexible gesture use
74 parallels that of other great apes^{32, 33, 34}. This suggests that social propensities can be fully expressed
75 in captivity, as individuals do not need to be solitary in order to obtain sufficient food, whereas in the
76 wild they may have fewer interaction opportunities and communication is hampered by arboreality
77 and obscuring vegetation. In addition, mothers are the predominant communication partner of infant
78 orang-utans in the wild^{35, 36}, so that there is a limited need for the production of extensive
79 communicative repertoires. There are no systematic wild-captive comparisons of apes'
80 communicative behaviour to date, but we assume that contrasts must be larger for orang-utans than
81 any other great ape taxon.

82

83 We examined non-vocal (i.e. gestural and facial) communicative acts of Bornean and Sumatran
84 orang-utans (*Pongo pygmaeus/abelii*) in two wild populations and five zoos. In a first step, we
85 established the repertoires and functions (presumed goals of communicative acts, with outcomes that
86 apparently satisfied the signaller) of orang-utans' non-vocal communicative acts, building on
87 previous work conducted on chimpanzees and captive orang-utans^{33, 37}, but separately for wild and
88 captive settings. We then tested several predictions about how setting affected individual repertoire
89 sizes and functional specificity of signal types, while controlling for important confounding variables
90 such as age-sex class and sampling effort. First, captivity should result in larger communicative
91 repertoires because of boosted territoriality, sociability and interaction rates. As a result, wild
92 repertoires should be a subset of the captive ones, except for those communicative acts that cannot be
93 expressed in captivity ("wild-only"). Second, we expect that the form of these communicative acts
94 expressed only in captivity should be tightly linked to the more terrestrial lifestyle or the increased

95 sociability, especially in the less terrestrial Sumatran orang-utans. Third, the “invention” of
96 additional signals in captivity should be accompanied by a wild-captive contrast in functional
97 specificity. We expect to find this contrast especially or even exclusively in Sumatran orang-utans,
98 because sociability and interaction rates are reportedly higher in the Northwest-Sumatran population
99 compared to the Bornean populations^{38,39}. The effect of this setting-species interaction on functional
100 specificity will allow us to derive important conclusions on the plasticity and flexibility underlying
101 communicative interaction in the *Pongo* genus.

102

103 **Results**

104 *Communicative acts across settings*

105 A total of 40 distinct signal types were identified across all settings, out of which 34 were observed
106 in Bornean (captive: N = 27, wild: N = 24) and 39 in Sumatran orang-utans (captive: N = 37, wild: N
107 = 32). Plotting the cumulative number of identified communicative acts over the course of the
108 observation period indicated that study groups have been sufficiently sampled to grasp complete
109 repertoires (Fig. 1, S1, S2, S3), except for two captive groups of Bornean orang-utans (Apenheul and
110 Cologne, see Fig. S1). In Table S1 we provide definitions for all coded behaviours and their relation
111 to previous work on orang-utans’ communicative repertoire. The majority of signal types (N) and
112 cases (n) consisted of manual (N = 19, n = 5106) and bodily signals (N = 18, n = 2212), whereas
113 considerably fewer facial acts (N = 3, n = 110) act were observed (see Tab. S2 for detailed overview
114 of signal presence in relation to settings, species, subjects and age classes). The relatively small
115 repertoire of facial signals may be partly due to our strict criteria of inclusion into the repertoire (see
116 methods).

117

118 We first tested the first prediction that captivity should result in enlarged communicative repertoires
119 at the aggregate level owing to boosted sociability and interaction rates. We found that the majority
120 of communicative acts ($N = 27$) was shared across orang-utan species and research settings, but that
121 9 communicative acts were restricted to captivity (e.g. “roll on back”, “throw object”, “somersault”,
122 see Fig. 2), and 2 to the wild (“loud scratch”, “shake object”, see Fig. 2), thus confirming the
123 prediction. Out of these, seven captivity-specific and one wild-specific acts were observed in the
124 Sumatran species only (e.g. “rub on body”, “head-butt”, “shake object”), whereas one behaviour
125 (“spin”) was observed in captive Borneans only (see Tab. S2 for a detailed overview communicative
126 acts across settings and species). A more conservative way of testing the prediction is by producing a
127 list based on all previous studies. We found that three of the communicative acts we found only in
128 captive settings (“throw object”, “rise up”) or wild settings (“shake object”), were also observed in
129 other species-setting combinations in other studies, which leaves at least seven captivity-only acts
130 and one wild-only act (see Tab. S3, note that Cartmill & Byrne [2010] do not specify which gestures
131 were observed in which orang-utan species). This more conservative test thus also confirms the
132 prediction.

133

134 To ensure that these differences between captivity and the wild do not reflect differences in social
135 opportunities (e.g. with regard to the availability same-age play partners), we compiled separate play
136 repertoires for mother-offspring (for which there is no change in partner availability between natural
137 and captive settings) versus same-aged interactions (Tab. S4). A graphical analysis revealed no
138 substantial difference between captive versus wild play repertoires with regard to mother-offspring
139 interactions (25 vs 24 in Sumatrans, 22 vs 18 in Borneans). For peer play interactions, repertoire
140 sizes apparently differed between settings for Sumatrans (26 vs. 19), but not Borneans (12 vs. 11).
141 Differences in repertoire sizes between captive and wild settings are thus not driven by partner
142 availability alone. Given that 13 communicative acts used in same-aged play interactions were

143 exclusively used in Sumatrans (Tab. S4), we suggest that repertoire size is driven more by social
144 opportunities in Sumatrans than in Borneans.

145

146 *Individual repertoire sizes across settings*

147 The average Bornean orang-utans had 1.9 more signal types in its repertoire (captive: mean \pm SD =
148 8.1 ± 3.8 , wild: 10 ± 4.7), while the average Sumatran had 6.8 more signal types (captive: mean \pm
149 $SD = 15.3 \pm 6.5$, wild: 8.5 ± 7.2), with a larger between-individual variation. With regard to age
150 classes, we found that younger immatures had the largest repertoire on average (mean \pm SD = $14.8 \pm$
151 5.9 , $N = 42$), followed by older immatures (10.1 ± 8 , $N = 41$), and adults (mean \pm SD = 7.3 ± 3.9 , N
152 = 37).

153

154 Using a linear mixed model (LMM), we tested how setting, species and confounding variables such
155 as sex, age class and sampling effort affected the number of communicative acts in individuals
156 recorded during the study (for details see methods). The full model including the key test predictors
157 (i.e. setting and species) fitted the data better than the null models irrespective of the subsets used
158 (LRT all individuals: $\chi^2_3 = 14.058$, $P = 0.003$, $N = 70$; individuals with > 50 interactions: $\chi^2_3 =$
159 15.131 , $P = 0.002$, $N = 44$). As expected, the number of communicative acts were strongly affected
160 by the number of samples contributed to the dataset (see Tab. 1 for output of the model using the
161 restricted dataset, Tab. S5 for the model including all individuals). Irrespective of the effects of
162 sampling effort, however, we found that captive individuals deployed a significantly larger variety of
163 communicative acts than their wild counterparts, again confirming our prediction. We also found that
164 individual repertoires of Sumatran individuals exceeded those of their Bornean counterparts (after
165 removing the non-significant interaction term, Tab. 1 a, Fig. 3 a, b). In addition, younger individuals
166 produced significantly more different communicative acts than adults (Tab. 1 a, Fig. S4). These

167 results are consistent with our expectations that young individuals (i.e. all immatures, but especially
168 those below the age of 5 years) regularly use a larger communicative set than adults, particularly for
169 the function of soliciting social play and food sharing. This is further supported by descriptive results
170 on presumed goals and outcomes of communicative acts (see ESM, Tab. S6, S7) suggesting that
171 interactions in both affiliative and conflict situations rather than co-locomotion or food-sharing
172 underlie the proliferation of communicative acts in captive settings.

173

174 *Functional specificity of communicative acts across settings*

175 We systematically tested the second prediction on functional specificity of communicative acts
176 depends on research setting and orang-utan species using a LMM, which also included confounding
177 variables such as outcome and sampling effort. The full model including the key test predictors (i.e.
178 setting, species, dominant outcome) fitted the data better than the null models (LRT: $\chi^2_3 = 22.612$, P
179 < 0.001 , $N = 114$). There was a significant interaction between research setting and orang-utan
180 species: while specificity scores in captivity did not differ between the species, we found a
181 significantly lower functional specificity in wild Sumatrans compared to their captive counterparts
182 (Fig. 4). Irrespective of this result, specificity was significantly higher for communicative acts
183 predominantly used to solicit play and observed in a larger number of subjects (Tab. 1 b). Our
184 findings thus support the prediction that larger repertoire sizes in captivity should be accompanied by
185 an increase in average functional specificity.

186

187 **Discussion**

188 Answering the question whether our primate relatives possess the behavioural plasticity, or creative
189 capacity, to complement their species-typical repertoires by inventing novel signals from scratch is
190 highly relevant to theories of language evolution. Yet, to date no study explicitly and systematically

191 examined communication systems of apes exposed to novel socioecological conditions relative to the
192 wild baseline situation. Here, we adopted a 2 x 2 comparative design, investigating repertoire sizes
193 and functional specificity of communicative acts in zoo-housed and wild groups of two different
194 orang-utan species with different sociability and terrestriality. By examining the captive-wild
195 contrast in these two related species we tested the prediction that captive environments favour the
196 emergence of novel communicative acts, which should also have higher functional specificity.
197 Moreover, comparing species differences related to differential sociability and terrestriality on one
198 hand, and setting on the other, we expected that Sumatran orang-utans, but not Borneans, would
199 show a wild-captive contrast in average functional specificity, offering insights into the degrees of
200 plasticity and flexibility underlying the communicative repertoires of orang-utans.

201

202 Consistent with our first prediction, communicative repertoires on both the aggregate and individual
203 level were larger in captivity as compared to the wild, even after controlling for the expected effects
204 of age class and sampling effort (i.e. irrespective of whether all or only highly sampled individuals
205 are included in the analysis). There may be some doubt that a single study can exhaustively sample
206 signal repertoires. We therefore also compared the captive-wild contrast for each species using all
207 available studies. This comparison supported the conclusions based on our study, in that the actual
208 repertoire *composition* found in previous studies in the same setting and species revealed no major
209 differences (Tab. S2, S3). First, our own findings regarding zoo repertoires (i.e. 27 different
210 communicative acts in captive Borneans and 37 in captive Sumatrans, as compared to 24 and 32
211 communicative acts in the wild, respectively) are broadly consistent with the available systematic
212 studies in single settings. Liebal and colleagues³², studying two captive groups of Sumatran orang-
213 utans, reported a repertoire of 34 signal types (29 gestures, and 5 facial expressions). Like them, we
214 found that the majority of communicative acts were used to solicit social play and food transfers.
215 Cartmill & Byrne³³, examining two zoo groups of Bornean and one group of Sumatran orang-utans,

216 identified 38 types of gesture and facial expressions that allowed the analysis of “intentional
217 meaning”. Second, the first systematic study on mother-offspring gesture use among wild orang-
218 utans, conducted at the Bornean population of Sabangau Forest, identified 21 gesture types that met
219 the criteria for inclusion into the repertoire ³⁵. With 24 different observed communicative acts
220 observed in our study population at Tuanan, it seems like the inclusion of communicative
221 interactions outside the mother-offspring bond does not result in a substantially larger repertoire size.
222 Thus, we can conclude that moving wild orang-utans into captivity leads to a 20 to 25% increase (i.e.
223 7 to 9 acts “gained”, 1 to 2 acts “lost”) in their repertoire of communicative acts.

224

225 The second prediction we made was that the form of these communicative acts expressed only in
226 captivity should be tightly linked to the increased sociability and more terrestrial lifestyle. As
227 expected, differences in repertoire size were particularly pronounced for presumed goals related to
228 seeking body contact (“Play/affiliate”, “Groom”, “Sexual contact”) and social conflict (“Move
229 away” and “Stop action”). Interaction rates with these outcomes are greatly boosted in captivity,
230 where a more differentiated use of bodily communication is both enabled and required ¹⁰. Captive
231 facilities are stable, plentiful and predator-free environments that may provide opportunities for, and
232 even require (e.g. due to increasing conflict with limited space) signal inventions and innovations,
233 just like they foster innovations in general ^{40,41}. Our findings thus provide direct evidence that the
234 new environments we have created for great apes boost the invention of new signals, which may
235 spread through social learning. Indeed, captive settings in general have generated extensive and
236 convincing evidence for invented (“species-atypical”) signalling, encompassing novel pant-hoot
237 variants ⁴², and “whistling” ¹⁵, as well as pointing with hands and fingers ^{43,44}, “raspberries” and
238 “extended grunts” in chimpanzees ¹⁶. Although detailed captive-wild comparisons are, to our
239 knowledge, so far lacking for other great apes, wild-captive contrasts are probably larger in orang-

240 utans than any other great ape taxon. In conclusion, our results support the notion that the new
241 opportunities and needs linked to captivity may lead to a proliferation of signal invention.

242

243 We also expected that the form of these communicative acts expressed only in captivity are linked to
244 a more terrestrial lifestyle. Indeed, we found that the communicative acts that are exclusively (or
245 overwhelmingly) produced in captive settings are strongly linked to the more terrestrial nature of
246 their artificial habitat: “somersaults”, “spitting”, “head-stands”, communicative acts that involve
247 either the ground or objects obtained from the ground, would be very difficult to perform by wild
248 orang-utans with their purely (Sumatra) or predominantly Borneo: ⁴⁵ arboreal lifestyle. This setting
249 effect is not attributable to the presence of certain interaction partners alone: by comparing the
250 repertoires for mother-offspring and peer play interactions we demonstrated that differences between
251 interaction dyads with regard to wild-captive contrasts were only strong in Sumatran orang-utans. It
252 thus appears that the new affordances of captive settings, on top of the elevated exposure to certain
253 social contexts, enabled orang-utans to better exploit their (communicative) motion spectrum,
254 resulting in novel communicative movements that may independently and predictably such as
255 spitting as an attention-getter, see ⁴⁶ be invented in several captive colonies and species. This also
256 confirms earlier reports making the case that the complex individual-based fission fusion structure of
257 orang-utans and their sophisticated social-cognitive skills seem to be reflected in a highly variable
258 communicative repertoire ^{32, 47}, illustrating their remarkable behavioural plasticity.

259

260 Finally, we predicted that the additional signals in captivity should be accompanied by an increase in
261 functional specificity. In line with our predictions, we found that Sumatrans in the wild exhibited a
262 lower average functional specificity compared to their captive counterparts, while average functional
263 specificity in captivity did not differ between the species. When comparing Sumatrans’

264 communicative acts used only in captivity (“invented signals”) with those used in both research
265 settings, captivity-only acts appeared to be on average more functionally specific (although the small
266 sample prevented inferential analyses). In other words, wild Sumatrans seem to use their
267 communicative acts more flexibly (i.e. redundantly) across presumed goals than in captivity, which
268 appears to be largely due to captive Sumatrans’ use of invented context-dependent, and therefore
269 functionally specific acts (i.e. those that have “tight meanings” according to ³³) not present in the
270 wild repertoire. In contrast, the relatively low interactions rates (due to few social opportunities) of
271 wild Bornean orang-utans ^{38, 39, 48} seem to be reflected in a lesser need to use signals flexibly across
272 contexts. Together, these results corroborate our expectation that average functional specificity
273 increased with repertoire size in captive Sumatran, though not Bornean orang-utans.

274

275 To convey a message that can be understood by a targeted recipient, an intentional agent may use
276 two alternative “strategies”. First, she can use one and the same communicative act for several
277 different functions, relying on context or other information (e.g. possibly age difference or sex
278 relative to recipient) to disambiguate between ambiguous meanings. This “flexible” communicative
279 strategy produces redundancy in the communicative repertoire. Alternatively, she can use a
280 communicative behaviour that is specific to one interaction outcome – and, if not available, invent
281 one for which naïve recipients (over repeated instances of interaction) infer their meaning from
282 context and reactions, which they may subsequently use in exactly the same contexts with exactly the
283 same function as their original inventor. This “plastic” communicative strategy produces productivity
284 in the communicative repertoire. Sumatran orang-utans in the wild seem to rely somewhat more on
285 the flexibility option; their captive counterparts, however, rely more on the plasticity option because
286 repeated interactions with the same partners in captivity allow them to establish novel signal
287 meanings more rapidly. This outcome is expected because novel signals are most likely to be
288 understood and thus maintained when they are highly context-specific.

289

290 We argue that distinguishing species-typical from invented communicative acts matters greatly for
291 current debates on language origins see also ¹⁰. Language reflects extreme communicative plasticity.
292 Words that make up language are predominantly invented noises used intentionally, and the
293 productivity feature of language fundamentally relies on the ability to produce such new noises,
294 which are used intentionally and rapidly acquire a shared meaning due to their high context-
295 specificity. Functionally specific signals are often more effective and efficient in complex
296 interactional exchanges (including language), because they are less dependent on context and thus
297 less ambiguous. Reliance on context may be less favourable with increasing message complexity
298 (multiple intertwining messages), because it increases both (i) the risk of misunderstanding, and (ii)
299 the “decoding work” necessary for the recipient, and thus the risk that the signal is ignored.

300

301 Although our knowledge of the taxonomic distribution of invented signals is still incomplete, they
302 are so far reported almost exclusively for great apes. Ongoing work supports this pattern, in that
303 great apes are increasingly documented to make up new vocal e.g. ^{15, 16, 49} and gestural e.g. ^{18, 50}
304 ‘signals’ in the novel conditions of captivity, whereas reports from other taxa are rare but see e.g. ^{51,}
305 ^{52, 53, 54}. Such communicative creativity may therefore be most common in, or even limited to, species
306 with intentional communication. These findings imply that once the conditions were in place that
307 favoured the open-ended use of invented expressions, our hominin ancestors readily responded to
308 this opportunity, because they could build on a long evolutionary history of communicative
309 creativity. This might explain why language evolved in the hominin lineage and not others that found
310 themselves in similar conditions (e.g. those canids that also rely on interdependent foraging and
311 cooperative breeding).

312

313 **Materials and Methods**

314 *Data collection*

315 Data were collected at two field sites and five captive facilities (zoos). We observed wild orang-utans
316 at the long-term research sites of *Suaq Balimbing* (03°02'N; 97°25'E, Gunung Leuser National Park,
317 South Aceh, Indonesia) and *Tuanan* (02°15'S; 114°44'E, Mawas Reserve, Central Kalimantan,
318 Indonesia), on a population of wild Sumatran (*Pongo abelii*) and Bornean orang-utans (*Pongo*
319 *pygmaeus wurmbii*), respectively. Both study sites consist mainly of peat swamp forest and show
320 high orang-utan densities, with 7 individuals per km² at *Suaq* and 4 at *Tuanan*^{55,56}. Captive Bornean
321 orang-utans were observed at the zoos of Cologne and Münster, and at Apenheul (Apeldoorn), while
322 Sumatran orang-utans were observed at the zoo of Zurich and at Hellabrunn (Munich; see EEP
323 studbook for details on captive groups; Becker 2016). While captive Sumatran orang-utans were
324 housed in groups of nine individuals each, captive Bornean groups were smaller (on average four
325 individuals, with the one in Apenheul including only a mother and her dependent and independent
326 offspring). Signallers included in this study consisted of 33 Bornean (21 wild/12 captive) and 38
327 Sumatran orang-utans (20 wild/18 captive; see Tab. S8 for detailed information on subjects and
328 group compositions).

329

330 Focal observations were conducted between November 2017 and October 2018 (*Suaq Balimbing*:
331 November 2017 – October 2018; *Tuanan*: January 2018 – July 2018, European zoos: January 2018 –
332 June 2018). At the two field sites, these observations consisted of full (nest-to-nest) or partial follows
333 (e.g. nest-to-lost or found-to-nest) of mother-infant units, whereas in zoos 6-hour focal follows were
334 conducted. Two different behavioural sampling methods were combined: First, presumable intra-
335 specific communicative interactions of all observed social interactions of the focal either as signaller
336 or receiver with all partners ($N = 7137$ acts), and among other conspecifics ($N = 888$ acts) present

337 were recorded using a digital High-Definition camera (Panasonic HC-VXF 999 or Canon Legria HF
338 M41) with an external directional microphone (Sennheiser MKE600 or ME66/K6), enabling
339 recordings of high-quality footage. In captive settings with glass barriers, we also used a Zoom H1
340 Handy recorder that was placed in background areas of the enclosure whenever possible. Second,
341 using instantaneous scan sampling at ten-minute intervals, we recorded complementary data on the
342 activity of the focal individual, the distance and identity of all association partners, and in case of
343 social interactions the interaction partner as well as several other parameters. During ca. 1600 hours
344 of focal observations, we video-recorded more than 6300 communicative interactions.

345

346 *Coding procedure*

347 A total of 2655 high-quality recordings of orang-utan interactions (wild: 1643, captive: 1012) were
348 coded using the program BORIS version 7.0.4.⁵⁸ We designed a coding scheme to enable the
349 analysis of presumably communicative acts directed at conspecifics (i.e. behaviours that apparently
350 served to elicit a behavioural change in the recipient and were mechanically ineffective i.e. achieve a
351 presumed goal without physical force; see also³³. Manual, bodily, and facial acts were defined and
352 aligned (see Tab. S1) based on previous studies on orang-utan communication in captive^{26, 32, 33, 46}
353 and wild settings^{35, 36, 59, 60}. Comparing our dataset to this literature, we then identified the subset of
354 setting- and species-specific communicative acts. Although we also coded vocalizations based on
355 field studies⁶¹, we did not include vocalizations in the analyses of repertoire and functional
356 specificity as we could not equally pick up soft, low-frequency sounds in captive and wild settings,
357 which hampered the fine-grained comparison across settings. For each communicative act, we coded
358 the following “modifiers”: presumed goal following the distinction of³³, outcome, and other
359 variables not directly relevant in this study (see Tab. S9 for levels and definitions of all coded
360 variables). To ensure inter-observer reliability, we evaluated the coding performance of all observers

361 with alternating datasets using the Cohen's Kappa coefficient⁶² during an initial training period and
362 at regular intervals afterwards. Trained observers (MF, NB, CF, CW, LM, MJ) proceeded with video
363 coding only if at least a 'good' level ($\kappa \geq 0.75$) of agreement was found for signal type, articulator,
364 sensory modality, context, and response. For our repertoire analyses, we plotted the cumulative
365 number of communicative behaviours over the number of coded interactions for each study group
366 (Fig. S1, S2) and for a subset of highly sampled individuals (Fig. S3), to estimate how many
367 observations are necessary to grasp the repertoire of these groups/individuals as indicated by an
368 asymptote. Communicative acts were counted as part of individuals' repertoire only when observed
369 at least twice per subject.

370

371 To analyse functional specificity, we focused on goal-outcome matches³³ or apparently satisfactory
372 outcomes³⁷, that is, whether the interaction outcome aligned with presumed goals identified by
373 observers. We considered only those signal types that were produced at least three times towards a
374 particular interaction outcome cf.³⁷. We defined functional specificity depending on how often a
375 communicative act was produced towards an apparently satisfactory outcome (ASO), adopting the
376 definitions of Cartmill and Byrne³³. Signal types that were used mainly towards a single interaction
377 outcome, i.e. more than 70% of the time, were defined as having "tight meanings". Signal types used
378 frequently towards a single ASO, i.e. 50–70% of the time, were defined as having "loose meanings".
379 Finally, signal types that were used less than 50% of the time towards a single ASO were classified
380 as having "ambiguous meanings". For instance, "somersault" was exclusively produced to initiate
381 "Play/affiliate" interactions (specificity value of 1, tight meaning), whereas "touch" was produced
382 towards several different interaction outcomes, e.g. "Play/affiliate", "Share food/object" and "Co-
383 locomote" (specificity values < 0.7 , ambiguous or loose meaning).

384

385 *Statistical analyses*

386 We ran two separate linear mixed models LMMs;⁶³ with a Gaussian error structure and identity link
387 function to examine sources of variation in (a) individual communicative repertoires (i.e. number of
388 signal types used at least twice) and (b) specificity in signal function. We used LMMs rather than
389 GLMMs in this study because it has recently been shown that linear models are more robust to
390 violations of distributional assumptions^{64, 65}. We ran model (a) for two subsets of our data: first,
391 including all individuals regardless of sample size; second, including only those individuals that
392 contributed more than 50 communicative acts to the dataset (as the graphical inspection of asymptote
393 plots in Fig. S3 suggested that this is a representative number to estimate individual repertoire sizes).

394

395 In model (a), which had individual repertoire size as response variable, we included research setting
396 (2 levels: captive, wild) and orang-utan species (2 levels: Bornean, Sumatran) as our key test
397 predictors. Because we assumed that the effect of research setting might depend on genetic
398 predisposition (i.e. species), we included the interaction between these two variables into our model.
399 Moreover, immature individuals often contribute the majority of both signal cases and types², for
400 reviews see³¹ and the composition of study groups differed with regard to age-sex classes, hence we
401 made sure that age class was taken into account in our analyses. We included the following variables
402 as additional fixed effects (control predictors) into the models: subjects' age class (3 levels: "adult":
403 females > 15 years, males > 16 years; "older immature": independent and dependent immature > 5
404 years of age, "younger immature": dependent immature < 5 years of age), sex (2 levels: female,
405 male), the number of interaction outcomes the subject communicated for at least twice (range = 1-6,
406 only four outcomes were coded in captive Borneans), and the number of observations (range = 5-
407 467). To control for repeated measurements within the same sampling unit, group identity was

408 treated as random effect. To keep type 1 error rates at the nominal level of 5%, we also included all
409 relevant random slopes components within group ID ⁶⁶.

410

411 In model (b), which had specificity in signal function as response variable, we included orang-utan
412 species (two levels: Bornean, Sumatran), research setting (two levels: captive, wild) and dominant
413 outcome (two levels: play, non-play), and the interaction between setting and species as our key test
414 predictors. To control for confounding effects of sampling effort, the number of subjects contributing
415 to the use of a signal type (range = 1–21) and the number of observations (range = 1–787) in the
416 respective setting as additional fixed effects (i.e. control predictors). To control for repeated
417 observations of the same signal types across settings, signal type was treated as random effect ⁶⁷.

418

419 All models were implemented in R (v3.4.1, ⁶⁸) using the function *glmer* of the package lme4 ⁶⁹. To
420 control for collinearity, we determined the Variance Inflation Factors VIF; ^{70,71} from a model
421 including only the fixed main effects using the function *vif* of the R package car ⁷². This revealed no
422 collinearity issues (maximum VIF = 2.8). Prior to running the models, we log-transformed the
423 response variables and the control variables relating to sampling effort (number of
424 observations/subjects), to achieve an approximately symmetrical distribution and avoid influential
425 cases.). To test the overall significance of our key test predictors ^{73,74}, we compared the full models
426 with the respective null models comprising only the control predictors as well as all random effects
427 using a likelihood ratio test ⁷⁵. Tests of the individual fixed effects were derived using likelihood
428 ratio tests (R function *drop1* with argument “test” set to “Chisq”).

429

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455

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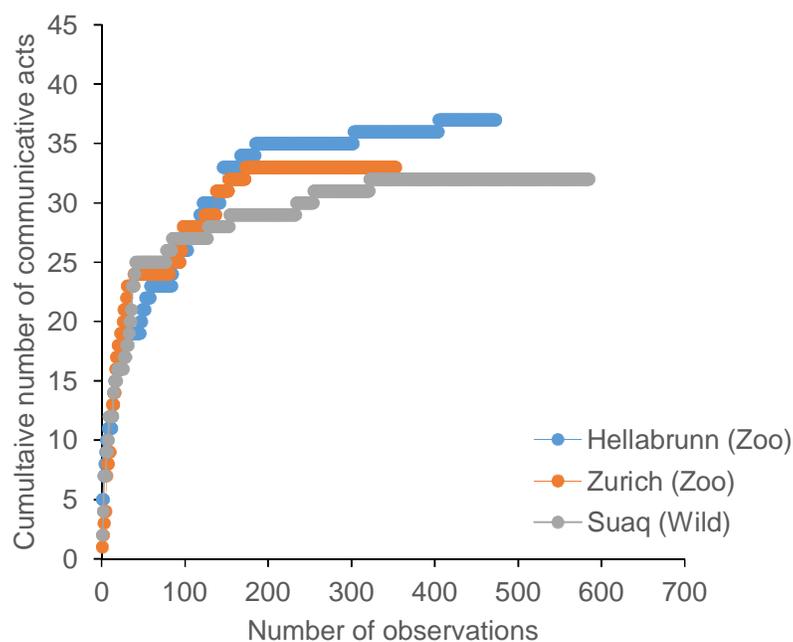
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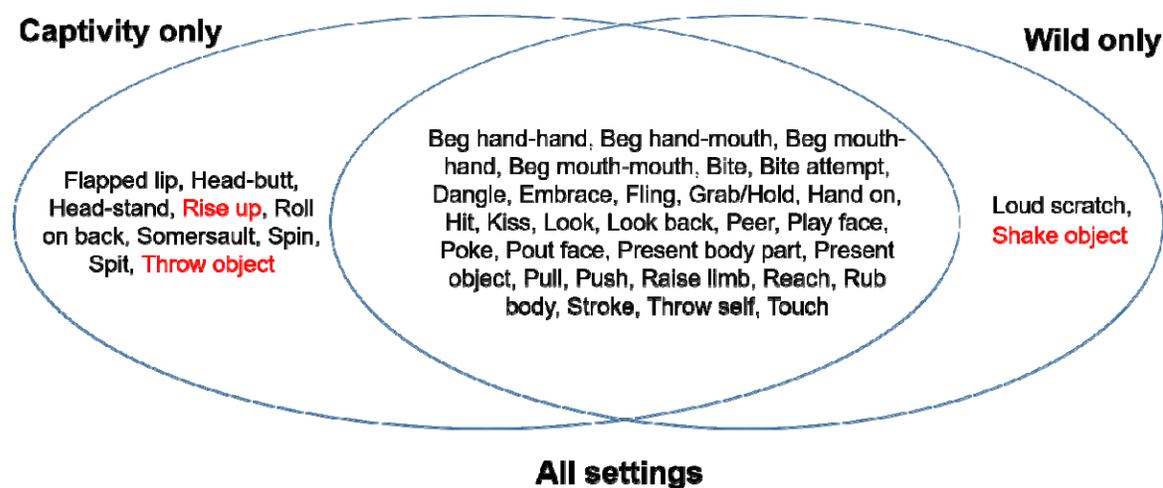
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688 **Figures and Tables**



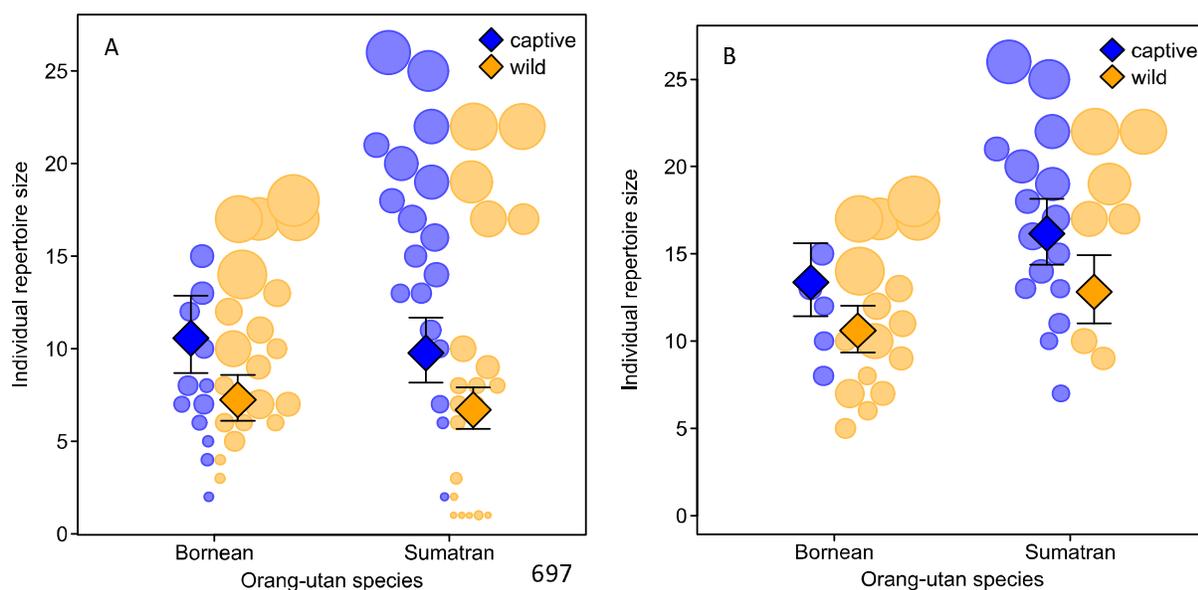
690 **Fig. 1. Cumulative number of identified communicative acts over observation time.** Asymptotes
691 are depicted separately for the captive subjects (Hellabrunn, Zurich) and wild populations (Suaq) of
692 Sumatran orang-utans in this study.



694 **Fig. 2. Overview of communicative acts observed only in different research settings.**

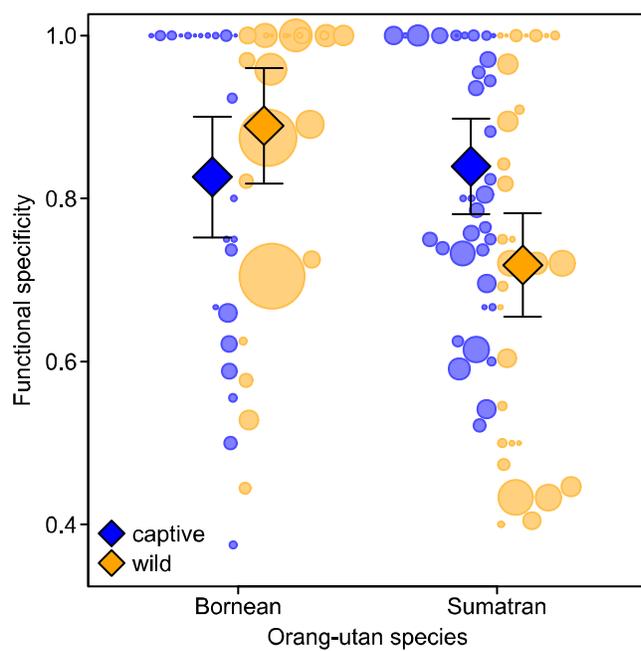
695 Communicative acts observed in the contrasting setting by other studies are marked in red.

696



698 **Fig. 3. Number of observed types of communicative acts per individual as a function of**
699 **research setting and orang-utan species, with (A) all subjects included, and (B) restricted to**
700 **subjects with > 50 samples. Circles represent different individuals with area corresponding to sample**
701 **size, Diamonds depict model estimates with 95% confidence intervals (all other variables centered to**
702 **a mean of zero).**

703



704

705 **Fig. 4. Functional specificity of communicative acts as a function of research setting and orang-**
706 **utan species.** Circles represent different signal types with area corresponding to sample size,
707 diamonds depict model estimates with 95% confidence intervals (all other variables centered to a
708 mean of zero).

709 **Tab. 1. Effects of research setting, orang-utan species, and control variables on (a) repertoire**
 710 **size of individuals (N = 44), and (b) functional specificity of communicative acts (N = 114),**
 711 derived using LMMs with a Gaussian error structure and identity link function. Significant effects (P
 712 < 0.05) are depicted in italics.

(a) Repertoire size	Estimate	SE	χ^2_1	P
Intercept	0.453	0.227	-	-
<i>Setting [wild]</i>	<i>-0.29</i>	<i>0.069</i>	<i>12.727</i>	<i><0.001</i>
<i>Species [Sumatran]</i>	<i>0.148</i>	<i>0.061</i>	<i>6.641</i>	<i>0.010</i>
<i>Age class [young imm.]</i>	<i>0.314</i>	<i>0.076</i>	<i>14.571</i>	<i><0.001</i>
Age class [old imm.]	0.243	0.138	3.396	0.065
Sex [male]	-0.039	0.064	0.223	0.637
No. functions	0.058	0.03	3.654	0.056
<i>Log (no. observations)</i>	<i>0.361</i>	<i>0.05</i>	<i>39.426</i>	<i><0.001</i>
(b) Functional specificity				
Intercept	0.898	0.06	-	-
Setting [wild]	0.059	0.043	-	-
Species [Sumatran]	0.002	0.039	-	-
<i>Dominant outcome [play]</i>	<i>0.095</i>	<i>0.038</i>	<i>5.911</i>	<i>0.015</i>
Log (no. observations)	0.004	0.019	0.043	0.836
<i>Log (no. subjects)</i>	<i>-0.072</i>	<i>0.034</i>	<i>4.578</i>	<i>0.032</i>
<i>Setting x species</i>	<i>-0.175</i>	<i>0.055</i>	<i>10.395</i>	<i>0.001</i>

713

714