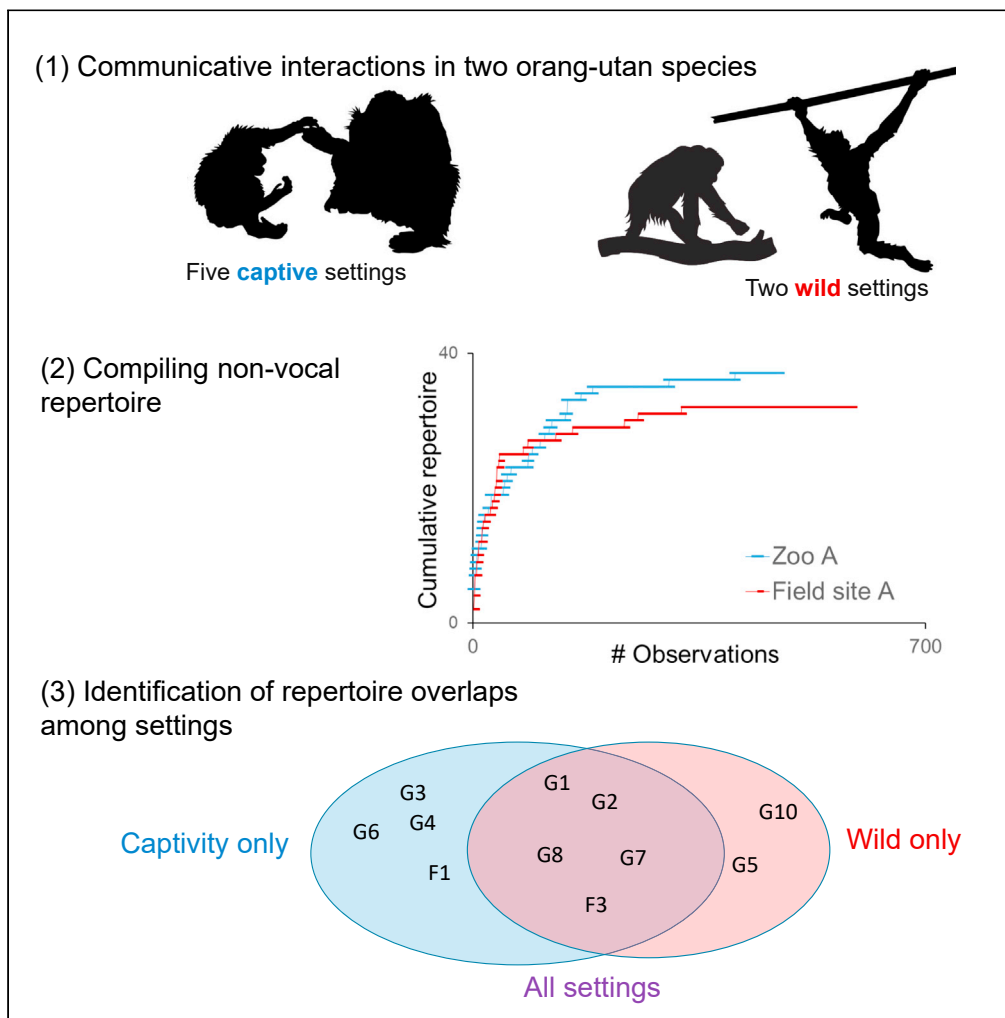


Article

Orangutans have larger gestural repertoires in captivity than in the wild—A case of weak innovation?



Marlen Fröhlich,
Natasha
Bartolotta,
Caroline Fryns, ...,
Caroline Schuppli,
Maria A. van
Noordwijk, Carel
P. van Schaik

marlen.froehlich@uzh.ch

Highlights

We studied wild-captive contrasts in gestural repertoires in two orangutan species

Individual and group-level repertoires were larger in captivity than in wild

Only in Sumatrans, functional specificity was higher in captivity than in wild

Some of orangutans' captivity-specific signals may qualify as weak innovations

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Article

Orangutans have larger gestural repertoires in captivity than in the wild—A case of weak innovation?

Marlen Fröhlich,^{1,8,*} Natasha Bartolotta,¹ Caroline Fryns,^{1,2} Colin Wagner,³ Laurene Momon,³ Marvin Jaffrezic,³ Tatang Mitra Setia,⁴ Caroline Schuppli,^{1,5} Maria A. van Noordwijk,^{1,7} and Carel P. van Schaik^{1,6,7}

SUMMARY

Whether nonhuman species can change their communicative repertoire in response to socio-ecological environments has critical implications for communicative innovativeness prior to the emergence of human language, with its unparalleled productivity. Here, we use a comparative sample of wild and zoo-housed orangutans of two species (*Pongo abelii*, *Pongo pygmaeus*) to assess the effect of the wild-captive contrast on repertoires of gestures and facial expressions. We find that repertoires on both the individual and population levels are larger in captive than in wild settings, regardless of species, age class, or sampling effort. In the more sociable Sumatran species, dominant use of signals toward single out-comes was also higher in captive settings. We thus conclude that orangutans exposed to more sociable and terrestrial conditions evince behavioral plasticity, in that they produce additional innate or innovated signals that are highly functionally specific. These findings suggest a latent capacity for innovativeness in these apes' communicative repertoires.

INTRODUCTION

Innovativeness is considered the engine of behavioral change in populations and thus pertinent to the study of animal culture and intelligence (Ramsey et al., 2007; Reader and Laland, 2003). Originally defined by Kummer and Goodall (1985) as “a solution to a novel problem or a novel solution to an old one”, there is no consensus on how novel or distinctive from species-typical behavior a trait needs to be to qualify as innovation. Nowadays ethologists widely agree that behaviors exist along a continuum in which the influence of internal (genetic) or external inputs varies in strength (Eibl-Eibesfeldt, 1975; Hinde, 1970). Accordingly, Ramsey et al. (2007) have suggested that there is an innovation gradient: at one end of the gradient, we find fully fledged inventions that tend to be rare, conspicuous, and cognitively demanding. At the other end are weak innovations, that is, behaviors that are partially, but not entirely, environmentally induced or socially learnt. For some groups of large and long-lived animal species, such as great apes, the modification of behavioral repertoires through prior experiences may be more likely, and the extent of innovativeness larger, compared with other animal taxa. This notion is supported by exceptional degrees of behavioral flexibility and ontogenetic plasticity reported for hominid species (Bandini and Harrison, 2020; Manrique et al., 2013; van Schaik et al., 2006).

Does this greater degree of innovativeness also extend to communicative behavior? If this is the case, it would seem less coincidental that language, with its remarkable productivity (Hockett, 1960), emerged in the hominid lineage. For instance, an early study by Kummer and Kurt (1965) showed that, of 68 social signals, 9 were not observed in the wild, providing perhaps the first evidence for innovations or “functional elaborations” in communication (e.g., including a gesture that invites infant to be carried). Nonetheless, the current consensus is that the vast majority of facial, vocal, and gestural expressions in non-human species has evolved through natural selection over long periods of time and have become innate. Thus, the ability to produce them arises spontaneously during ontogeny, and only their use is often fine-tuned by practice (Byrne et al., 2017; Cheney and Seyfarth, 2018; Wegdell et al., 2019). However, accumulating evidence suggests that the socio-ecological environment can profoundly impact the use of communicative signals throughout primate lifetimes (for reviews see Fröhlich and Hobaiter, 2018; Liebal et al., 2013; Snowdon and Hausberger, 1997). For example, recent research on great apes, our closest living relatives, has shown that some gestures and sounds are apparently innovated

¹Department of Anthropology, University of Zurich, 8057 Zurich, Switzerland

²Institute of Biology, University of Neuchâtel, 2000 Neuchâtel, Switzerland

³Département Ecologie, Physiologie et Ethologie, University of Strasbourg, 67037 Strasbourg, France

⁴Fakultas Biologi, Universitas Nasional, 12520 Jakarta Selatan, Indonesia

⁵Development and Evolution of Cognition Research Group, Max Planck Institute of Animal Behavior, 78467 Konstanz, Germany

⁶Center for the Interdisciplinary Study of Language Evolution (ISLE), University of Zurich, 8050 Zurich, Switzerland

⁷Comparative Socioecology Research Group, Max Planck Institute of Animal Behavior, 78467 Konstanz, Germany

⁸Lead contact

*Correspondence: marlen.froehlich@uzh.ch
<https://doi.org/10.1016/j.isci.2021.103304>



and maintained over time (Fröhlich et al., 2016; Halina et al., 2013; Hardus et al., 2009b; Hopkins et al., 2007; Tomasello et al., 1997; Wich et al., 2012; Wich et al., 2009), and play the same role in the communication process as evolved signals do—we could thus call them signal innovations (Fröhlich and van Schaik, 2020). This work therefore suggests that it may be timely to distinguish between innate animal signals and those that are acquired developmentally (see Bard et al., 2014 for a similar conclusion, finding that some gestures are clearly genetically predisposed, whereas others are not).

Targeted long-term studies to estimate the extent of ontogenetic plasticity (including “innovativeness”) in great apes’ communicative behavior are difficult. Here, we therefore rely on an alternative approach: we systematically compare the same species living in the wild and in man-made, artificial habitats in captivity (Fröhlich and van Schaik, 2020; Kummer and Goodall, 1985). This contrast permits a direct test of how repertoires respond to the differences in the socio-ecological environment. In captivity, individuals face less competition for food, have more spare time, are closer together, are often more visible to each other and more on the ground than in the wild (Fröhlich and van Schaik, 2018; Liebal et al., 2013). Especially in semi-solitary, fission-fusion species such as orangutans (*Pongo* spp.), interaction rates in contexts such as social play, grooming, conflict situations, and mating are much larger in captive settings (e.g., Fröhlich et al., 2021; Kopp and Liebal, 2018; Maple, 1980; Zucker et al., 1978), which may favor the production of additional signals (including both “signals” in the strict evolutionary sense, and those communicative acts that qualify as weak innovations; see also Fröhlich and van Schaik, 2020) that are completely absent in the wild and thus cause differences in the communicative repertoires of individuals and groups.

The captive-wild contrast also allows us to examine an additional, related issue: the extent to which the functional specificity (i.e., the predominance of particular interaction outcomes) of signals depends on the socio-ecological environment in which they are used (although we must also take into account that the prevalence of certain contexts also varies between research settings). First, signals of any sensory modality can vary in their *meaning* (function) between individuals and social groups (Boesch, 1996; Fichtel and Van Schaik, 2006; Salmi and Muñoz, 2020). This kind of change may reflect the presence of behavioral plasticity, high levels of which are a prerequisite for the generation of novel signals (i.e., signal innovations). Second, signals specific to one research setting (e.g., captivity) can differ in functional specificity from those present in all settings. Hence, the aim of the present study was to examine repertoires and functional specificity of close-range signals.

We conducted this study in both wild and captive populations of orangutans, a great ape genus ideal for this avenue of research, because the captive-wild contrast in social behavior is arguably greater than for any other taxon. First, systematic studies on the gestural repertoire of captive orangutans have demonstrated a propensity for elaborate and flexible gesture use that parallels that of other great apes (Cartmill and Byrne, 2010; Cartmill and Byrne, 2007; Liebal et al., 2006). These findings suggest that social propensities may be more fully expressed in captivity, as individuals do not need to avoid associations with conspecifics in order to obtain sufficient food, unlike in the wild, where most close-range communication (i.e., visual, tactile, and audible) is predominantly between mothers and their infants (Bard, 1992; Fröhlich et al., 2019; Knox et al., 2019). This continuous sociality may facilitate the production of more extensive communicative repertoires. Second, visual communication is less hampered by arboreality and obscuring vegetation. We also compared the captivity effect separately for Sumatran and Bornean orangutans. Sociability and interaction rates are reportedly higher in the Northwest Sumatran population than the Bornean populations (Fröhlich et al., 2020; van Schaik, 1999), and studying both species in both research settings (i.e., adopting a 2 x 2 design) permits teasing apart the effect of intrinsic differences in social tolerance from wild-captive contrasts on the production and use of additional innate or innovated signals.

We examined non-vocal (i.e., gestural and facial) signals of Bornean and Sumatran orangutans (*Pongo pygmaeus* and *Pongo abelii*) in two wild populations and five zoos. In a preparatory step, we established the repertoires and functions (presumed goals of communicative acts, with outcomes that apparently satisfied the signaler; Cartmill and Byrne, 2010; Hobaiter and Byrne, 2014) of orangutans’ gestural and facial signals separately for wild and captive settings, by pooling our results and previous work conducted on chimpanzees and captive orangutans. We then tested several predictions about how setting affected repertoire sizes and functional specificity of signal types.

First, captivity should result in larger communicative repertoires because of increased terrestriality, sociability, and interaction rates. These conditions may enable the production of signals not feasible or useful in

natural environments (Marler, 1965), resulting in the use of “weak innovations” (Ramsey et al., 2007), which are easily reproduced by different individuals under suitable conditions (Lehner et al., 2010; Tennie et al., 2020). Thus, wild repertoires should be largely a subset of the captive ones, but there also may be signal types that are not expressed in captivity (“wild-only”), e.g., due to environmental constraints, but we expect that this effect is modest for the gestures and facial expressions examined here.

Second, we expect that the form of signal types expressed only in captivity should be tightly linked to the more terrestrial lifestyle or the increased sociability (Becker, 1984; Jantschke, 1972; Maple, 1980; Perkins, 1992; Wilson, 1982; Zucker et al., 1978), especially in the less terrestrial Sumatran orangutans. Specifically, we would expect a proliferation of signals whose expression requires flat substrates and involves mobile objects, and in communicative contexts that do not occur on a daily basis in wild settings (e.g., social play and conflict beyond the mother-offspring dyad). We would thus predict that gestural repertoires of two individuals of the same species living in the same research settings (i.e., either captivity or wild, within-setting similarity) exhibit a larger degree of overlap than those of two individuals living in different settings (i.e., captivity versus wild, between-setting similarity). This should be a direct consequence of adaptation to the specific socio-ecological environments individuals interact (i.e., immediate responses, behavioral flexibility) and grow up in (i.e., developmental responses, ontogenetic plasticity).

Third, this greater variety of signals in captivity may be accompanied by higher functional specificity in this setting (estimated by a preponderance of specific outcomes for a given signal, in contrast to multiple outcomes), whereas we may find more flexible (or redundant) use of signals (i.e., one and the same act for several different functions) in natural environments. This is because the additional acts (“weak innovations”) observed in captivity may be tightly linked to the specific interactions we expect to see more often in this artificial environment, especially social play (see above).

In all comparisons, we controlled for confounding variables such as age-sex class (young apes regularly use a larger communicative set than adults, particularly for soliciting social play and food transfers; Call and Tomasello, 2007; Liebal et al., 2013) and sampling effort (an obvious driver in the estimation of individual repertoire sizes). The effect of the setting-species interaction on repertoires and functional specificity will allow us to draw important conclusions regarding the extent of communicative plasticity and flexibility in the *Pongo* genus.

RESULTS

Production of gestures and facial expressions across settings

Among 11,035 coded gestural and facial signals (see Table 1 for numbers in relation to species and setting), we identified 41 distinct signal types across all settings, of which 39 were observed in Bornean (captive: $N = 38$, wild: $N = 24$) and 39 in Sumatran orangutans (captive: $N = 37$, wild: $N = 32$). In Table S1 we provide definitions for all coded behaviors and their relation to previous work on orangutans’ gestural repertoires. Plotting the cumulative number of identified signals over the course of the observation period indicated that study groups have been sufficiently sampled to capture complete site-specific repertoires (Figure 1). The majority of non-vocal signal types consisted of manual (total: $N = 20$; captive: $N = 18$; wild: $N = 18$) and bodily gestures (total: $N = 18$; captive: $N = 18$; wild: $N = 12$), whereas considerably fewer facial expressions (total: $N = 3$; captive: $N = 3$; wild: $N = 2$) were observed (see Table 1 for detailed overview of signals in relation to settings, species, subjects, and age classes). The relatively small repertoire of facial signals may be partly due to our strict criteria of inclusion into the repertoire (see STAR methods), so these findings should be viewed with caution.

The first prediction was that captivity should result in enlarged communicative repertoires at the aggregate level owing to boosted sociability and interaction rates. The majority of signal types ($N = 30$) was observed (i.e., coded more than once) in both research settings. However, nine gesture types were restricted to captivity (e.g., “roll on back,” “throw object,” “somersault”), and two to the wild (“loud scratch,” “shake object,” see Table 1 and Figure 2 for overview of gestures and facial expressions used across settings), thus confirming the prediction. In addition, another five gesture types were observed very rarely (i.e., less than five times) in wild compared with captive settings (“head-butt,” “hit,” “look back at,” “present object,” “throw self,” Table 1). We thus find that gestural communication repertoires expressed by zoo-housed orangutans are about 20% greater than those of their wild counterparts.

Table 1. Overview of produced signal types in relation to setting, species, and age class

Signal	Signal type	No subjects	Age class	Dominant outcome	Bornean		Sumatran		Total
					Captive	Wild	Captive	Wild	
Beg hand-hand	Manual	30	Ad, Oi, Yi	FS	45	152	55	98	350
Beg hand-mouth	Manual	27	Ad, Oi, Yi	FS	27	82	64	73	246
Beg mouth-hand	Bodily	27	Ad, Oi, Yi	FS	26	69	76	28	199
Beg mouth-mouth	Bodily	26	Ad, Oi, Yi	FS	45	38	136	24	243
Bite	Bodily	39	Ad, Oi, Yi	PL	117	264	54	8	443
Bite attempt	Bodily	41	Ad, Oi, Yi	PL	83	141	61	24	309
Dangle	Bodily	24	Ad, Oi, Yi	PL	307	36	49	65	457
Embrace	Manual	14	Ad, Oi, Yi	PL	9	8	23	18	58
Flap lip	Facial	3	Ad, Oi, Yi	ST			11		11
Fling	Manual	20	Ad, Oi, Yi	PL	20	4	31	37	92
Grab/hold	Manual	64	Ad, Oi, Yi	PL	795	787	178	348	2,108
Hand on	Manual	43	Ad, Oi, Yi	PL	215	177	29	148	569
Head-butt	Bodily	6	Ad, Oi, Yi	PL	(1)		29	3	32
Head-stand	Bodily	5	Ad, Oi, Yi	PL	16		4	(1)	20
Hit	Manual	16	Ad, Oi, Yi	PL	78		83	4	165
Hit ground/object	Manual	3	Ad, Oi, Yi	PL	3				3
Kiss	Bodily	24	Ad, Oi, Yi	PL	29	57	62	2	150
Look at	Bodily	46	Ad, Oi, Yi	PL	175	40	72	210	497
Look back at	Bodily	14	Ad, Oi, Yi	PL	19		26	2	47
Loud scratch	Manual	7	Ad, Oi, Yi	JT		5		29	34
Peer	Bodily	34	Ad, Oi, Yi	FS	211	39	223	88	561
Play face	Facial	18	Ad, Oi, Yi	PL	64	10	46	20	140
Poke	Manual	25	Ad, Oi, Yi	PL	124	36	87	3	250
Pout face	Facial	3	Ad, Oi, Yi	PL	4	10	6		20
Present body part	Manual	29	Ad, Oi, Yi	GR, JT	7	87	28	26	148
Present object	Manual	10	Ad, Oi, Yi	PL	40	(1)	14	4	58
Pull	Manual	53	Ad, Oi, Yi	PL, FS	178	110	222	161	671
Push	Manual	46	Ad, Oi, Yi	ST, PL	164	42	95	115	416
Raise limb	Manual	18	Ad, Oi, Yi	PL	187		14	10	211
Reach	Manual	41	Ad, Oi, Yi	PL, FS	202	18	88	107	415
Rise up	Bodily	8	Ad, Oi, Yi	PL, JT	64		3		67
Roll on back	Bodily	11	Ad, Oi, Yi	PL	119		2		121
Rub body	Bodily	12	Ad, Oi, Yi	PL, SX	2		60	27	89
Shake object	Manual	1	Ad, Oi, Yi	PL				5	5
Somersault	Bodily	5	Ad, Oi	PL	56		4		60
Spin	Bodily	3	Oi, Yi	PL	8				8
Spit	Bodily	2	Oi, Yi	PL	(1)		5		5
Stroke	Manual	8	Ad, Oi	PL	(1)		13	5	18
Throw object	Manual	10	Ad, Oi, Yi	PL	65		10		75
Throw self	Bodily	14	Ad, Oi	PL	135		58	2	195
Touch	Manual	60	Ad, Oi	PL	503	598	156	214	1,471
Total					4,142	2,810	2,177	1,906	11,035

Ad, adult; Oi, older immature; Yi, younger immature; FS, Share food/object; GR, Groom; JT, Co-locomote; PL, Play/affiliate; SX, Sexual contact; ST, stop action; blue: captivity only; orange: wild only. See also [Table S1](#).

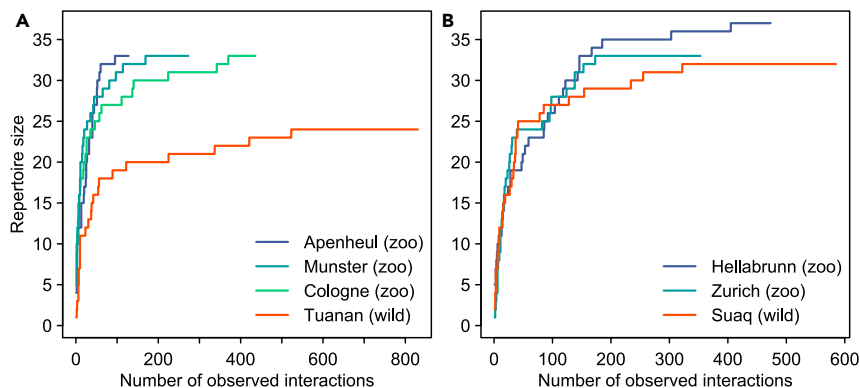


Figure 1. Cumulative number of identified signal types in (A) Bornean and (B) Sumatran orangutans over consecutively observed interactions

(A and B) Asymptotes are depicted separately for the captive groups (A: Apenheul, Cologne, Munster, B: Hellabrunn, Zurich) and wild populations (A: Tuanan, B: Suaq) in this study. See also [Figure S1](#).

A more conservative way of testing the prediction is by producing a list based on all previous studies. Our own findings regarding zoo repertoires (i.e., 38 different types of non-vocal signal types in captive Borneans and 37 in captive Sumatrans, as compared with 24 and 32 signal types in the wild, respectively) are broadly consistent with the available systematic studies in single settings. Liebal and colleagues (2006), studying two captive groups of Sumatran orangutans, reported a repertoire of 34 signal types (29 gestures, and 5 facial expressions). Like them, we found that the majority of communicative acts were used to solicit social play and food transfers. [Cartmill and Byrne \(2010\)](#), examining two zoo groups of Bornean and one group of Sumatran orangutans, identified 38 types of gesture and facial expressions that allowed the analysis of “intentional meaning.” For wild settings, a recent systematic study on mother-offspring gesture use among wild orangutans, conducted at the Bornean population of Sabangau Forest, identified 21 gesture types that met the criteria for inclusion into the repertoire ([Knox et al., 2019](#)). With 24 different observed signal types observed in our study population at Tuanan, it thus seems like communicative interactions outside the mother-offspring bond do not result in a substantially larger repertoire size. Three of the gesture types we found only in captive (“hit ground/object,” “throw object”) or wild settings (“shake object”) were also observed in other species-setting combinations in other studies, which leaves at least seven captivity-only acts and one wild-only act (see [Table S2](#); note that [Cartmill and Byrne \(2010\)](#) do not specify which gestures were observed in which orangutan species). However, it should be noted that our study was restricted to intra-specific interactions, whereas other studies in the wild presumably included displays directed at humans ([MacKinnon, 1974](#); [Rijksen, 1978](#)). This more conservative comparison, assessing whether the captivity-only acts of our study were observed in the wild in previous studies and *vice versa*, thus also confirms the prediction that gestural/facial repertoires in captivity should be larger.

To ensure that differences between captivity and the wild do not merely reflect differences in social opportunities (e.g., with regard to the availability of same-age play partners), we compiled separate play repertoires for mother-offspring, for which there is no change in partner availability between natural and captive settings, versus same-aged interactions ([Table S3](#)). For both orangutan species, we found that play solicitation repertoires observed in mother-offspring and peer interactions did not significantly differ depending on research setting (Fisher’s exact test, Borneans: $P = 0.072$, Sumatrans: $P = 0.408$). This shows that differences in repertoire sizes between captive and wild settings are not mainly driven by partner availability.

Individual repertoire sizes

The repertoire differences should also hold at the individual level, even if sampling issues might weaken the effect of setting and species. Using a generalized linear mixed model (GLMM), we tested how setting, species, and important confounding variables such as age class and sampling effort affected the repertoire size of gestures and facial expressions in individuals recorded during the study (for details see [STAR methods](#)). The full model including the key test predictors (i.e., setting and species) fitted the data better than the null models irrespective of the subsets of individuals included (likelihood ratio test [LRT] only highly sampled individuals: $\chi^2_3 = 26.011$, $P < 0.001$, $N = 57$; LRT all individuals: $\chi^2_3 = 25.007$, $P < 0.001$, $N = 71$). As expected, individual repertoire sizes were strongly affected by the number of samples contributed to the dataset (see

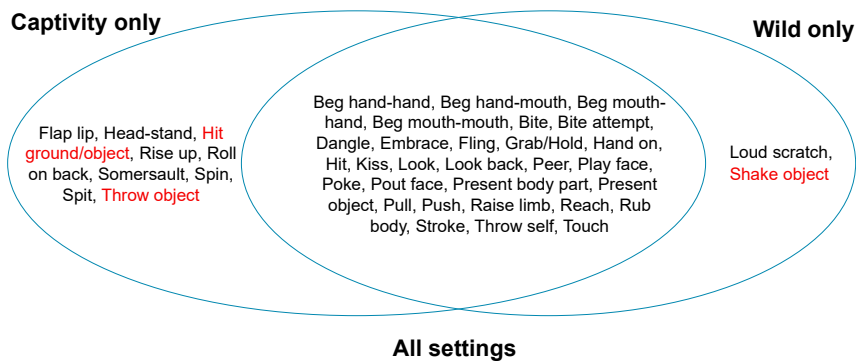


Figure 2. Overview of signal types observed across research settings

Gesture types observed in the contrasting setting by other studies are marked in red. See also [Table S2](#).

[Table 1](#)). After removing the non-significant interaction term, we found that captive individuals exhibited a significantly larger variety of gestural and facial signals than their wild counterparts regardless of individual sample size ([Table 2](#), [Figure 3](#)), again confirming our prediction. We also found that both immature age classes produced significantly more signal types than adults ([Tables 2](#), [S4](#), [Figure S2](#)). These results are consistent with previous work showing that immature apes regularly use a larger gestural set than adults (e.g., [Liebal et al., 2006](#)). For effects of non-significant predictors see [Table 2](#). A less conservative analysis, including all individuals regardless of contributed samples, yielded essentially the same results ([Table S4](#)). Descriptive results indicated no difference between the sexes: female orangutans used an average of 12.3 different signal types (SD = 6.7, $N = 42$), whereas males had 12.9 different types (SD = 8.9, $N = 29$). Our descriptive results on presumed goals of signal types broken up by species and setting (see [Table S5](#)) suggest that the higher rate of interactions in both affiliative and conflict situations rather than co-locomotion or food-sharing underlies the proliferation of signal types in captive settings. We thus conclude that captive Borneans and Sumatrans also have larger individual repertoire sizes, even if broken down by age classes (see [Table S6](#)).

Repertoire similarity within and between settings

Next, we investigated whether the composition of individual repertoires systematically differed between captivity and the wild. To this end, we calculated Dice coefficients and conducted matrix permutations tests to analyze whether within-setting repertoire similarity (i.e., similarity of repertoires between two individuals living in the same research setting, e.g., captivity) differs from between-setting repertoire similarity, separately for mothers and young immatures and separately for Bornean and Sumatran orangutans. For both age classes in both species, we found that within-setting similarity of communicative repertoires was significantly larger than between-setting similarity (Bornean mothers: mean Within- $D_c = 0.73$, Between- $D_c = 0.57$, $P < 0.001$; Bornean immatures: Within- $D_c = 0.76$, Between- $D_c = 0.61$, $P < 0.001$; Sumatran mothers: Within- $D_c = 0.62$, Between- $D_c = 0.53$, $P = 0.025$; Sumatran immatures: Within- $D_c = 0.73$, Between- $D_c = 0.61$, $P < 0.001$; see [Figure 4](#)). In contrast, degrees of repertoire overlaps within captivity and within the wild were largely similar, except in Sumatran mothers (Bornean mothers: mean Within- D_c (wild) = 0.72, Within- D_c (captive) = 0.76, $P = 0.662$; Bornean immatures: Within- D_c (wild) = 0.73, Within- D_c (captive) = 0.85, $P = 0.959$; Sumatran mothers: Within- D_c (wild) = 0.81, Within- D_c (captive) = 0.51, $P < 0.001$; Sumatran immatures: Within- D_c (wild) = 0.72, Within- D_c (captive) = 0.73, $P = 0.595$). This provides further support for the notion that communicative repertoires used in the wild and in captivity systematically differ in composition and that the additional signal types produced in captivity were often the same ones.

Functional specificity of signal types

Finally, we tested the second prediction that the functional specificity of signal types (i.e., proportion specifying the dominance of single interaction outcomes, see [STAR methods](#)) depends on research setting and orangutan species. On average, functional specificity of signal types was 0.82 ± 0.19 across all settings and both species. It was somewhat lower in captive than in wild individuals among Borneans (captive: 0.85 ± 0.18 ; wild: 0.88 ± 0.18) and higher among Sumatrans (captive: 0.82 ± 0.16 ; wild: 0.72 ± 0.22). Using a GLMM, the full model including the key test predictors (i.e., setting, species) fitted the data better than the null models (LRT: $\chi^2_3 = 126.511$, $P < 0.001$, $N = 128$). Specifically, there was a significant interaction

Table 2. Effects of research setting, orangutan species, and control variables on (a) repertoire size of individuals (N = 57) and (b) functional specificity of signal types (N = 114), derived using GLMMs

	Estimate	SE	χ^2_1	P
(a) Repertoire size				
Intercept	2.519	0.085	–	–
Setting [wild]	<i>–0.344</i>	<i>0.077</i>	<i>20.430</i>	<i><0.001</i>
Species [Sumatran]	0.103	0.087	1.350	0.245
Age class [young imm.]	<i>0.37</i>	<i>0.098</i>	<i>14.051</i>	<i><0.001</i>
Age class [old imm.]	<i>0.308</i>	<i>0.108</i>	<i>5.875</i>	<i>0.015</i>
No. observations	<i>0.178</i>	<i>0.037</i>	<i>22.813</i>	<i><0.001</i>
(b) Functional specificity				
Intercept	2.691	0.272	–	–
Setting [wild]	<i>0.299</i>	<i>0.135</i>	–	–
Species [Sumatran]	<i>–0.407</i>	<i>0.152</i>	–	–
Dominant outcome [play]	<i>–0.304</i>	<i>0.157</i>	<i>3.721</i>	<i>0.054</i>
No. subjects	<i>–0.182</i>	<i>0.085</i>	<i>4.563</i>	<i>0.033</i>
No. observations	<i>–0.004</i>	<i>0.037</i>	<i>0.012</i>	<i>0.911</i>
Setting x species	<i>–1.083</i>	<i>0.189</i>	<i>33.210</i>	<i><0.001</i>

Significant effects ($p < 0.05$) are depicted in italics. See also [Table S4](#).

between research setting and orangutan species: post hoc Sidak tests revealed that functional specificity of signal types in wild Sumatrans was significantly lower compared with their captive counterparts (estimate \pm standard error = 0.784 ± 0.12 , $Z = 6.556$, $P < 0.001$) and compared with wild Borneans (1.49 ± 0.144 , $Z = 10.348$, $P < 0.001$; see [Figure 5](#)). In contrast, functional specificity was significantly lower in captive Bornean orangutans compared with their wild counterparts (-0.299 ± 0.135 , $Z = -2.224$, $P = 0.026$) but higher compared with captive Sumatrans (0.407 ± 0.152 , $Z = 2.678$, $P = 0.007$), although these effects were smaller (see [Figure 5](#)). Regardless of the species-setting effects, specificity was significantly higher for signal types observed in a larger number of subjects ([Table 2](#)).

In Sumatrans, functional specificity of captivity-only acts ($N = 7$) was on average 0.9 ± 0.16 , as opposed to 0.76 ± 0.19 for signal types used in both wild and captive settings ($N = 30$). In Borneans, functional specificity of captivity-only acts ($N = 7$) was also higher than for acts used in both settings ($N = 30$; 0.97 ± 0.06 versus 0.85 ± 0.19). These descriptive results (the sample size prevents meaningful inferential analyses) also suggest that both species use signal types with higher functional specificity in captive than in wild settings, which seems to be driven by those acts used only in captivity. We also note that functional specificity seems to be on average higher in Borneans versus Sumatrans, which may be due to fewer social opportunities both in the wild and in captivity, and thus less exposure to the full range of social contexts.

Our findings thus support the prediction that larger repertoire sizes in captivity should be accompanied by greater average functional specificity compared with wild settings. However, the slightly lower specificity for captive Borneans than their wild counterparts was not expected and may have been caused by contextual differences in the respective research environments.

DISCUSSION

To explore the extent of communicative plasticity and innovativeness in gestural and facial signals, we here adopted a 2×2 design, investigating repertoire sizes and functional specificity of signal types in zoo-housed and wild groups of two different orangutan species diverging in sociability. By examining the captive-wild contrast in these two related species we found that captive environments favor larger and different repertoires of signals (including additional signal types that may represent “weak innovations”) among orangutans. We also found that this difference was reflected in larger within- versus between-setting repertoire overlaps between individuals. Moreover, considering species differences related to differential sociability and terrestriality on one hand, and setting on the other, we found that Sumatran orangutans, but not Borneans, showed a pronounced wild-captive contrast in the functional specificity of signals,

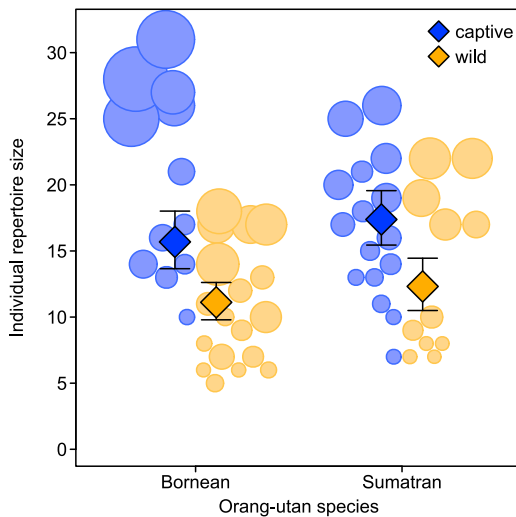


Figure 3. Number of observed signal types per individual as a function of research setting and orangutan species, restricted to subjects with >40 samples

Circles represent different individuals with area corresponding to sample size; diamonds depict model estimates with 95% confidence intervals (all other variables centered to a mean of zero). See also Figure S2.

offering insights into the degrees of “communicative innovativeness” (i.e., additional signals) versus behavioral flexibility (i.e., using the same signal type for different social goals and vice versa) underlying the communicative repertoires of orangutans.

Consistent with our first prediction, communicative repertoires on both the aggregate and individual levels were larger in captivity as compared with the wild, even after controlling for the expected effects of age class and sampling effort (i.e., irrespective of whether all or only highly sampled individuals are included in the analysis). There may be some doubt that a single study can exhaustively sample signal repertoires. We therefore also compared the captive-wild contrast for each species using all available studies. This comparison corroborated the conclusions based on our study, in that the actual repertoire *composition* found in previous studies in the same setting and species revealed no major differences (Table S2). From the results of this and previous studies, we can conclude that moving wild orangutans into captivity leads to a 20% to 25% increase (i.e., 7–9 acts “gained,” 1–2 acts “lost”) in their non-vocal communicative repertoire.

The second prediction we made was that the form of these communicative acts expressed only in captivity should be tightly linked to the increased sociability and more terrestrial lifestyle that comes with it. As predicted, differences in repertoire size were particularly pronounced for presumed goals related to seeking body contact (e.g., soliciting “Play/affiliate,” “Groom,” “Sexual contact”) and social conflict (e.g., with the apparent aim to have the recipient “Move away” or “Stop action”). Interaction rates involving these outcomes are greatly boosted in captivity, where a more differentiated use of bodily communication is both enabled (owing to the availability of even substrate) and required (to navigate social contexts uncommon in the wild; Fröhlich and van Schaik, 2020). This setting effect is not attributable to the presence of certain social partners alone: we demonstrated that wild-captive contrasts were strong for both mother-offspring and peer play interactions. Captive facilities are stable, plentiful, and predator-free environments that may provide opportunities for, and even require (e.g., due to increasing conflict with limited space), weak signal innovations and modifications, just like they foster innovations in general (Lehner et al., 2010; van Schaik, 2016).

Our findings thus provide indirect evidence that the new environments we have created lead to the production of larger gestural and facial repertoires in orangutans, which may be linked to at least some degree of communicative innovativeness. Nonetheless, we cannot entirely rule out that a few of these additional signal types (e.g., rise up, flapped lip) may also be observed in wild individuals after more extensive research efforts. We may also have missed a specific part of the wild repertoire that is only produced in poor-visibility conditions such as nesting and copulation, but since these signals were also not recorded in captivity this does not affect the above conclusion. Other studies on captive apes have generated convincing evidence for specific, invented (“species-atypical”) signals, encompassing novel pant-hoot variants (Marshall et al., 1999), and “whistling” (Wich et al., 2009), as well as pointing with hands and fingers (Leavens and Hopkins, 1998; Leavens et al., 2010), “raspberries” and “extended grunts” (Hopkins et al., 2007). However, these novel signals were predominantly observed in direct interaction with human caretakers and thus potentially imitated from them. In conclusion,

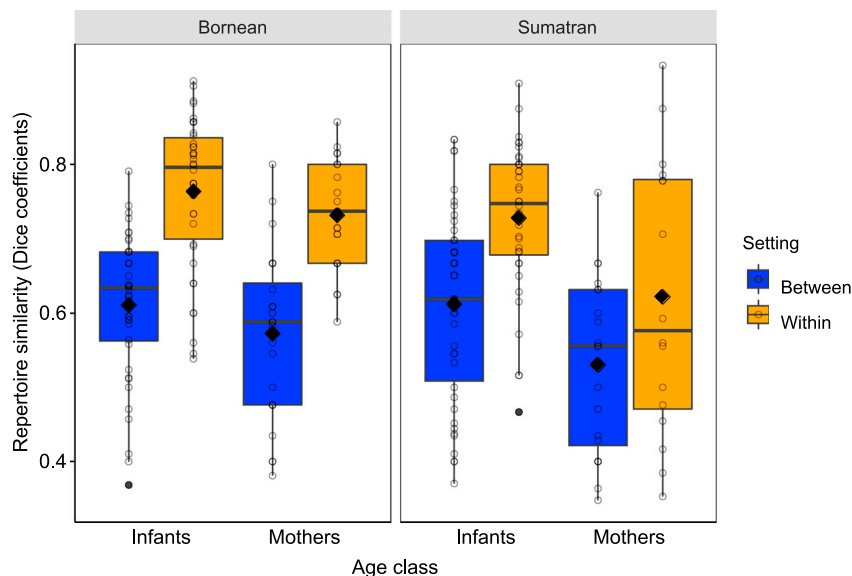


Figure 4. Repertoire similarity of two individuals living in different (“between”) and the same (“within”) research settings, separately for two age classes and both orangutan species

Indicated are dyadic coefficients (circles), population means (filled diamonds), medians (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines), and outliers (filled dots). Individuals have contributed to multiple data points.

our results support the notion that the socio-ecological conditions linked to captivity may lead to the production of additional innate or learned communicative utterances.

We also expected that the form of communicative acts expressed only in captivity are linked to the novel element of a more terrestrial lifestyle. Accordingly, repertoires of individuals living in the same setting should overlap more than those of individuals living in different settings. Indeed, we found that the signal types that are exclusively (or overwhelmingly) produced in captive settings are strongly linked to the more terrestrial nature of their artificial habitat: “somersaults”, “hit object”, “head-stands”; signal types that involve either the ground or objects obtained from the ground, would be very difficult or even impossible to produce by wild orangutans with their purely (Sumatra) or predominantly (Borneo: [Ashbury et al., 2015](#)) arboreal lifestyle. Moreover, we found a strikingly higher similarity of gestural and facial communication repertoires within settings (comparing dyads of the same setting) than between them (comparing dyads of different settings), for both age classes considered (mothers versus offspring) and both orangutan species (Bornean versus Sumatran). It thus appears that the new affordances of captive settings, on top of the elevated exposure to certain social contexts, enabled orangutans to better exploit their (communicative) motion spectrum, resulting in novel communicative movements that may independently and predictably be produced in several captive colonies and species (such as spitting as an attention-getter, see [Jantschke, 1972](#)). The wild-captive contrast in signal use also confirms earlier reports making the case that the complex individual-based fission fusion structure of orangutans and their sophisticated social-cognitive skills seem to be reflected in a highly variable communicative repertoire ([Liebal et al., 2006](#); [Maestripietri, 1999](#)).

Advocates of phylogenetic gesture origins may argue that those orangutan gestures observed only in captivity may in fact be “family-typical”, in that they are also found in the African apes (e.g., [Byrne et al., 2017](#); [Kersken et al., 2018](#)). If so, the absence of certain signals in wild orangutans would not mean that captivity-only signals are not part of the innate species repertoire, and thus zoo-housed orangutans would just exhibit gestures inherited from previous, less arboreal ancestral species. To us, however, this is a less parsimonious explanation for at least some of the terrestrial behavior patterns we have observed here, because a signal is defined not only by its looks or morphology but also (or even more so) by its function in communication or “meaning” ([Fröhlich and Hobaiter, 2018](#)). Somersaulting or spitting, for instance, may be found in playful contexts of many social mammals, but its successful use as a play solicitation gesture may still be largely learned during ontogeny.

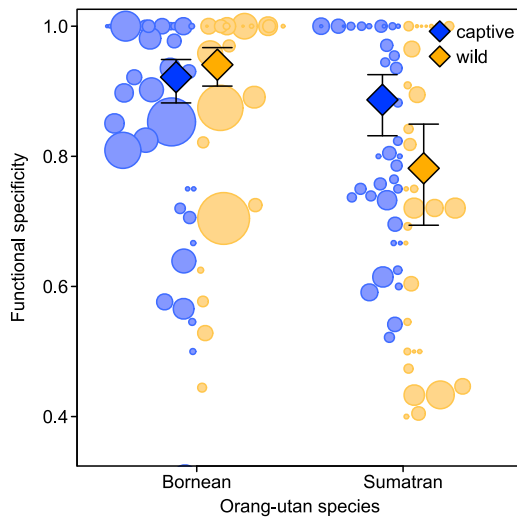


Figure 5. Functional specificity measures of signal types as a function of research setting and orangutan species

Circles represent different signal types with area corresponding to sample size; diamonds depict model estimates with 95% confidence intervals (all other variables centered to a mean of zero).

Finally, we predicted that the functional specificity of signals should also be larger in captivity compared with wild settings. In line with our predictions, we found that Sumatrans in the wild exhibited strikingly lower functional specificity scores compared with their captive counterparts, but the opposite effect was found for Bornean orangutans. When comparing Borneans' and Sumatrans' signal types used only in captivity with those used in both research settings, captivity-only acts were more functionally specific in both species (although the small sample and unbalanced data prevented inferential analyses). In other words, wild Sumatrans seem to use their signal types much more flexibly (and thus redundantly) across presumed goals than in captivity, which appears to be largely due to captive Sumatrans' use of additional functionally specific acts not present in the wild repertoire. In contrast, the relatively low interaction rates and fewer social opportunities of wild Bornean orangutans (Fröhlich et al., 2020; Mitra Setia et al., 2009; van Schaik, 1999) may be reflected in a lesser need to use signals flexibly across contexts (although social opportunities are not necessarily tightly linked to repertoire size). Thus, the species difference is mainly related to differences in functional specificity in the wild, not in captivity. Together, these results corroborate our expectation that average functional specificity increased with repertoire size in captive Sumatran, although not in Bornean, orangutans.

Our results and previous findings regarding communicative flexibility and development (e.g., Cheney and Seyfarth, 2018; Fröhlich and Hobaiter, 2018; Liebal et al., 2013) provide evidence for two forms of phenotypic plasticity in great ape communication: behavioral flexibility (immediate responses) and ontogenetic plasticity (developmental responses). On the immediate level, an intentional agent can flexibly communicate by using one and the same communicative act for several different functions (i.e., means-end dissociation), relying on situational context (possibly age difference or sex relative to recipient; Graham et al., 2020) to disambiguate between signals. This behavioral flexibility produces at least some redundancy in the communicative repertoire (Byrne et al., 2017), as we can see in our sample of wild Sumatran orangutans. On the developmental level, the intentional agent may either start to produce a new communicative behavior, from their species-specific repertoire not previously expressed due to environmental constraints, or, if not available, produce one for which naïve recipients (over repeated instances of interaction, e.g. through ontogenetic ritualization; Halina et al., 2013) infer their meaning from context and reactions. This ontogenetic plasticity may well produce higher functional specificity because novel signals may be more readily understood and thus maintained in the repertoire when they are highly functionally specific (Wheeler and Fischer, 2012). However, it could be argued that context is nearly always present in every-day usage of signals, and future studies may show that differences in functional specificity, in practice, need not correspond to varying levels of ambiguity. Moreover, we cannot rule out that our functional specificity measures also reflect differences in the socio-ecological environments to which the subjects in this study were exposed, so these findings have to be viewed with caution. If the signal types unique to captive settings qualify as innovations, they are surely of a "weak" nature (i.e., easily reinvented by individuals in the proper context; Ramsey et al., 2007). However, these weak innovations seem to be widespread in the great ape behavioral repertoire: experiments have shown repeatedly that many great ape innovations in the wild can readily be reproduced by captive ones when

suitable conditions are offered (Lehner et al., 2010; Tennie et al., 2020). Future research needs to look more thoroughly at between-individual versus within-individual variation in signal use, in order to provide more direct evidence that the captivity- or wild-specific gestures indeed qualify as innovations (as opposed to elements of a latent repertoire shared by all hominids).

Answering the question of whether our primate relatives possess the behavioral plasticity, or communicative creativity, to complement their species-typical repertoires by creating signals from scratch is highly relevant to theories of language evolution (see also Fröhlich and van Schaik, 2020), given that the productivity feature of language (the ability to create and understand novel utterances with novel meanings; Hockett, 1960) reflects extreme communicative plasticity. Although this study cannot provide direct evidence for productivity, our findings regarding behavioral plasticity (“weak inventions” sensu Ramsey et al., 2007) are nonetheless consistent with the view that apes possess a latent capacity for communicative innovativeness. So far, no study had explicitly and systematically examined communication systems of apes exposed to novel socioecological conditions relative to the wild baseline situation. Although our knowledge of the taxonomic distribution of signal innovation is still incomplete, this phenomenon is so far reported almost exclusively for great apes. Ongoing work supports this pattern, in that great apes are increasingly documented to make up new vocal (see above, and Tagliapietra et al., 2012) and gestural (e.g., Halina et al., 2013; Tomasello et al., 1994) signals in the novel conditions of captivity, whereas reports from other taxa are rare (but see, e.g., Garland et al., 2011; Grant and Grant, 1996; Moura, 2007; Perry et al., 2003). These findings imply that once the conditions were in place that favored the open-ended use of invented expressions, our hominin ancestors readily responded to this opportunity, because they could build on a long evolutionary history of communicative plasticity. This might explain why language evolved in the hominin lineage and not others that found themselves in similar conditions (e.g., reliance on interdependent foraging and cooperative breeding).

Limitations of the study

Our study has two important caveats. First, given that orangutans are arboreal primates, wild and captive settings differ profoundly in conditions for behavioral observation. Dense vegetation may have hampered the recording of subtle visual or acoustic communication, whereas the glass barriers of zoo enclosures often prevented the collection of sufficient high-quality data on vocal repertoires. We may also have missed a specific part of the wild repertoire (e.g., signals that are only produced in poor-visibility conditions such as nesting and copulation), but since these were also not recorded in captivity this does not affect the above conclusions. The future development of data recording technology (e.g., silent drones above canopy nests, enclosure-integrated cameras and microphones) may alleviate some of these difficulties. Second, captive orangutans may differ from their wild counterparts not only in general sociability and terrestriality but also in other opportunities and constraints. For instance, the functional specificity measures obtained in this study may also reflect differences in the specific contexts to which the subjects were exposed, so these findings have to be viewed with caution.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2021.103304>.

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AUTHOR CONTRIBUTIONS

M.F. and C.P.v.S. conceived the study. M.F. designed the project and collected, coded, and analyzed data. N.B., C.F., C.W., L.M., and M.J. helped to collect, curate, and code data. T.M.S., C.S., M.A.v.N., and C.P.v.S. provided resources. M.F. and C.P.v.S. wrote the manuscript with inputs from C.F., L.M., C.S., and M.A.v.N. All authors approved the submission of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We worked to ensure sex balance in the selection of non-human subjects. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list. The author list of this paper includes contributors from the location where the research was conducted who participated in the data collection, design, analysis, and/or interpretation of the work.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Repository data	This paper	https://doi.org/10.5281/zenodo.5561236
Experimental models: organisms/strains		
<i>Pongo abelii</i>	Housed at the zoos of Hellabrunn (Munich) and Zurich; wild population living in Gunung Leuser National Park, Northern Sumatra, Indonesia	N/A
<i>Pongo pygmaeus</i>	Housed at the zoos of Apenheul (Apeldoorn), Cologne and Munster; wild population living in Mawas Reserve, Central Kalimantan, Indonesia	N/A
Software and algorithms		
R Studio	R Development Core Team, 2020; R Foundation for statistical computing	https://www.r-project.org/
Custom R scripts	This paper	https://doi.org/10.5281/zenodo.5561236

RESOURCE AVAILABILITY

Lead contact

Information and requests for resources should be directed to and will be fulfilled by the lead contact, Marlen Fröhlich (marlen.froehlich@uzh.ch).

Materials availability

No new materials were generated in this study.

Data and code availability

- Data have been deposited at Zenodo and is publicly available as of the date of publication. DOI is listed in the [key resources table](#).
- All original code has been deposited at Zenodo and is publicly available as of the date of publication. DOI is listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Data were collected at two field sites and five captive facilities (zoos). We observed wild orang-utans at the long-term research sites of Suaq Balimbing (03°02'N; 97°25'E, Gunung Leuser National Park, South Aceh, Indonesia) and Tuanan (02°15'S; 114°44'E, Mawas Reserve, Central Kalimantan, Indonesia), in a population of wild Sumatran (*Pongo abelii*) and Bornean orang-utans (*Pongo pygmaeus wurmbii*), respectively. Both study sites consist mainly of peat swamp forest and show orang-utan densities of 7 individuals per km² at Suaq and 4 at Tuanan (Husson et al., 2009; Singleton et al., 2009). Captive Bornean orang-utans were observed at the zoos of Cologne and Munster, and at Apenheul (Apeldoorn), while Sumatran orang-utans were observed at the zoo of Zurich and at Hellabrunn (Munich; see EEP studbook for details on captive groups; Becker 2016). While captive Sumatran orang-utans were housed in groups of nine individuals each, captive Bornean groups were generally smaller and sometimes included only a mother and her offspring (e.g. Apenheul). Subjects (i.e. signallers) included in this study consisted of 33 Bornean (20 wild/13 captive) and 38 Sumatran orang-utans (20 wild/18 captive). Subjects consisted of 33 adults (26 females, 7 males) and 38 immatures (16 females, 22 males). Detailed information on subjects and group compositions is provided in [Table S7](#).

The following institutions granted permission to conduct research on wild orang-utans: the Indonesian State Ministry for Research and Technology (RISTEK, 398/SIP/FRP/E5/Dit.KI/XI/2017), the Indonesian Institute of Science (LIPI), the Directorate General of Natural Resources and Ecosystem Conservation – Ministry of Environment & Forestry of Indonesia (KSDAE-KLHK, SI.70/SET/HKST/Kum.I/II/2017), the Ministry of Internal Affairs, the Nature Conservation Agency of Central Kalimantan (BKSDA), the local governments in Central Kalimantan, the Kapuas Protection Forest Management Unit (KPHL), the Bornean Orang-utan Survival Foundation (BOSF) and MAWAS in Palangkaraya.

METHOD DETAILS

Data collection

Focal observations were conducted between November 2017 and October 2018 (Suaq Balimbing: November 2017 – October 2018; Tuanan: January 2018 – July 2018, European zoos: January 2018 – June 2018). At the two field sites, these observations consisted of full (nest-to-nest) or partial follows (e.g. nest-to-lost or found-to-nest) of mother-infant units, whereas in zoos 6-hour focal follows were conducted. Two different behavioural sampling methods were combined: First, presumable intra-specific communicative interactions of all observed social interactions of the focal either as signaller or receiver with all partners, and among other conspecifics present (if the focal was engaged in a non-social activity while still in full sight) were recorded using a digital High-Definition camera (Panasonic HC-VXF 999 or Canon Legria HF M41) with an external directional microphone (Sennheiser MKE600 or ME66/K6). In captive settings with glass barriers, we also used a Zoom H1 Handy recorder that was placed in background areas of the enclosure whenever possible. Second, using instantaneous scan sampling at ten-minute intervals, we recorded complementary data on the activity of the focal individual, the distance and identity of all association partners, and in case of social interactions the interaction partner as well as several other parameters. During ca. 1600 hours of focal observations, we video-recorded more than 6300 communicative interactions which were subsequently screened for good enough quality to ensure video coding.

Coding procedure

A total of 3014 high-quality recordings of orang-utan interactions (wild: 1354, captive: 1660) were coded using the program BORIS version 7.0.4. (Friard and Gamba, 2016). We designed a coding scheme to enable the analysis of presumably communicative acts directed at conspecifics (i.e. close-range social behaviours that apparently served to elicit a behavioural change in the recipient and were mechanically ineffective, thus excluding practical acts such as picking up an object or acts produced with physical force; Call and Tomasello, 2007; Cartmill and Byrne, 2010; Fröhlich et al., 2021). This resulted in the coding of 11,153 non-vocal communicative acts (i.e. potential gestures and facial expressions), of which 4939 (wild: 3476, captive: 1463) were produced within mother-offspring interactions, and 6214 (wild: 1248, captive: 4966) among other interaction dyads (see Table S8 for distribution across settings and species). Although we also coded vocalizations based on field studies (Hardus et al., 2009a), we did not include vocalizations in the analyses of repertoire and functional specificity as we could not equally pick up soft, low-frequency sounds in captive and wild settings, which hampered the fine-grained comparison across settings. Detailed results for sensory modalities and articulators involved, as well as the multisensory and multicomponent use of communicative acts have been reported elsewhere (Fröhlich et al., 2021). All individual gestures and facial expressions were defined and aligned based on previous studies on orang-utan intentional communication in captive (Cartmill and Byrne, 2010; Jantschke, 1972; Liebal et al., 2006; Zucker et al., 1978) and wild settings (Fröhlich et al., 2019; Knox et al., 2019; MacKinnon, 1974; Rijksen, 1978; see Table S1). Comparing our dataset to this literature, we then identified the subset of setting- and species-specific signal types.

For each gesture or facial expression, we also coded the presumed goal (following the distinction of Cartmill and Byrne, 2010) and apparently satisfactory outcome (i.e. whether signaller ceased communication and if it represented the signaller's plausible social goal, Hobaiter and Byrne, 2014; see Table S9 for levels and definitions), but also several other variables not directly relevant in this study. After an initial training period of two to four weeks, and afterwards in regular intervals (once a month), consistency of coding performance between at least two observers was evaluated with different sets of video recordings (10 to 20 clips each) using the Cohen's Kappa coefficient to ensure inter-coder reliability (Bakeman and Quera, 2011). Trained coders proceeded with video coding only if at least a 'good' level ($\kappa = 0.75$) of agreement was found for type of signal type, presumed goal, and interaction outcome.

Data processing

For our repertoire analyses, we plotted the cumulative number of communicative behaviours over the number of coded interactions for each study group (Figures 1 and 2) and for a subset of highly sampled individuals (Figure S1), to estimate how many observations are necessary to grasp the repertoire of these groups/individuals as indicated by an asymptote. Signal types were counted as part of an individual's repertoire only when observed at least twice per subject.

To analyse functional specificity, we considered only those signal types that were produced at least three times towards a particular interaction outcome (cf. Hobaiter and Byrne, 2014). We defined functional specificity depending on how often a signal type was produced towards a single apparently satisfactory outcome (ASO). For instance, "somersault" was exclusively produced to initiate "Play/affiliate" interactions (specificity value of 1), whereas "touch" was produced towards several different interaction outcomes, e.g. "Play/affiliate", "Share food/object" and "Co-locomote" (specificity values < 0.7).

Quantification and statistical analysis

We ran two separate generalized linear mixed models (GLMMs; Baayen, 2008) with a Poisson or binomial error structure, respectively, to examine sources of variation in (a) individual communicative repertoires (i.e. number of signal types used at least twice, for two different datasets: one including all individuals and one including only those that contributed at least 40 samples), and (b) signal types' specificity in function (i.e. the proportion of cases for which a signal type was used towards a single interaction outcome). In both models, we included research setting (2 levels: captive, wild) and orang-utan species (2 levels: Bornean, Sumatran) as our key test predictors. Because we assumed that the effect of research setting might depend on genetic predisposition (i.e. species), we also included the interaction between these two variables into our full model.

In model (a) testing individual repertoire size, we included the following variables as additional fixed effects (control predictors) into the models: subjects' age class (3 levels: "adult": females > 15 years, males > 16 years; "old immature": independent and dependent immature > 5 years of age, "young immature": dependent immature < 5 years of age), and the number of observations (range = 5–467; z-transformed). To control for repeated measurements within the same sampling unit, group ID was treated as random effect. We also included an observation level random effect, which models the extra-Poisson variation in the response variable using a random effect with a unique level for every data point (Gelman and Hill, 2006). We checked for overdispersion, revealing no issue (dispersion parameters < 1). To keep type 1 error rates at the nominal level of 5% (i.e. accounting for the non-independence of data points that pseudo-replicate slope information), we initially also included all relevant random slopes components within group ID (Schielzeth and Forstmeier, 2009). In model (b) testing functional specificity, we included the dominant outcome (2 levels: play, other; accounting for possibility that social opportunities differ between species and settings), number of subjects contributing to the use of a signal type (range = 1–21; z-transformed) and number of observations (range = 1–626; z-transformed) in the respective setting as control predictors. To control for repeated observations of the same signal types across settings, signal type was treated as random effect (Pinheiro and Bates, 2000).

All models were implemented in R (v4.0.3; R Development Core Team, 2020) using the function *glmer* of the package lme4 (Bates et al., 2014). To control for collinearity, we determined the Variance Inflation Factors (VIF; Field, 2005; Quinn and Keough, 2002) from a model including only the fixed main effects using the function *vif* of the R package car (Fox and Weisberg, 2011). This revealed no collinearity issues (maximum VIF = 1.6). To test whether the effects of our key test predictors were statistically significant (Forstmeier and Schielzeth, 2011; Mundry, 2014), we compared the full models with the respective null models comprising only the control predictors as well as all random effects using a likelihood ratio test (Dobson, 2002). To adjust for multiple comparisons, we tested interaction effects using pairwise contrasts with the function *lsmeans* (with argument "adjust" set to "sidak") of the package lsmeans. When non-significant, these interaction terms were removed before testing the individual fixed effects. Tests of the individual fixed effects were derived using likelihood ratio tests (R function *drop1* with argument "test" set to "Chisq").

To compare repertoire similarity within and between research settings, we calculated Dice coefficients (Dice, 1945) for each pairing of individuals with $D_C = (2C_{AB}) / (R_A + R_B)$, where C_{AB} is the number of signals observed in both individuals (A and B), while R_A and R_B are the number of signals in the repertoire of two

individuals A and B. The values range between 0 and 1: if two individuals have no signal types in common we get $D_C = 0$, whereas two identical signal repertoires correspond to $D_C = 1$ (see [Fröhlich et al., 2016](#); [Halina et al., 2013](#) for similar analyses). Because data points were non-independent as individuals contributed to multiple pairings, we conducted matrix permutation tests ($N = 1000$ permutations, significance level $\alpha = 0.025$) in R to analyse whether (i) individuals (i.e. mothers, dependent immatures) of the same settings share more signal types than individuals living in contrasting settings, and (ii) individuals living in captive settings have more dissimilar repertoires than individuals in wild settings. We only included subjects that contributed more than 40 samples, and only considered signal types that were used at least twice by each individual.