

ANTHROPOLOGY

Early sociability fosters later exploratory tendency in wild immature orangutans

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Exploration is essential for skill acquisition and strongly facilitates cognitive performance. In humans, it is widely known that exploration and later cognitive performance are highly dependent on early social inputs. Here, we aim to shed light on the evolutionary roots of this process by studying the effects of variation in opportunities for social learning on the exploratory tendency of immature orangutans (*Pongo* spp.) in nature. We based our analyses on mixed cross-sectional, longitudinal data of exploration by immatures and their mothers. Current exploration rates were correlated with levels of past experienced sociability, but not with current food abundance or with maternal condition, and only partly with genetic similarity. We conclude that the dependence of cognitive development on socially triggered exploration, which underlies the construction of cognitive skills such as intelligence, existed before the emergence of the human lineage.

INTRODUCTION

Comparative psychology has shown that many species can be compared not only on domain-specific but also on their domain-general cognitive abilities or intelligence, suggesting that the underlying cognitive capacity is an evolved trait and older than our own species (1). From an evolutionary perspective, cognitive capacities can only be favored by natural selection if they translate into adaptive skills. In any species, adult cognitive capacity will reflect genetic and developmental effects. However, the more intelligent a species is, the more incompetent its infants are at birth and the more they have to learn so as to acquire their extensive adult skill repertoires and behavioral flexibility (2, 3). This suggests that the developmental construction of intelligence and its underlying neurobiological substrate critically depends on the quantity and quality of inputs during ontogeny, be they from the social or nonsocial environment (4).

An individual's cognitive potential is translated into actual skills through exploration and practice, which can happen independently or be socially induced (by associating with, interacting with, or observing other individuals or their products) (5). Exploration is often called "latent learning" and is not only a key precondition for independent learning (learning by doing) but, because virtually all forms of social learning entail an element of independent trial and error (6–8), it is also critically involved in socially mediated learning (where attending to social cues triggers independent learning), arguably the most common type of social learning in nature (9). Individuals that explore more or more effectively should, therefore, be the best learners and so acquire the largest sets of learned skills. Moreover, the variability and persistence of an individual's exploration behavior are correlated with problem-solving ability and innovation probability in a variety of species (10–14), indicating that it is also the precursor of innovations made independently by individuals. The tendency of human infants to explore the physical properties of objects or the surrounding environment has been shown to be linked with learning ability, general current cognitive performance, and later cognitive development (12, 14). Exploration in human children has also been

shown to be dependent on an intrinsic underlying motivation—curiosity—which most likely acted as a catalyst for turning our species' unmatched innovation potential into an unprecedented level of cultural evolution (15). Curiosity may reflect internal predispositions or organizational effects of external inputs.

Given the key role of exploration in the skill acquisition process and the evolution of human cognition, it is crucial to identify the conditions that foster it. In general, exploratory tendency could be regulated by immediate, activating factors in an individual's environment, social inputs, or genetic predispositions, which may also interact.

For humans, there is ample evidence that social inputs during early childhood determine within-population variation in cognitive development at least as much as, if not more than, genetic predispositions do (16). Children growing up with severely limited social inputs later show deficits in various cognitive domains (17), as well as correlated physiological and anatomical changes in the brain (18). Even subtle differences in the frequency and quality of social inputs during early childhood, such as the amount of social interactions or the degree and consistency of responsiveness of parents or caretakers, substantially affect cognitive development (19). Thus, social inputs appear to be necessary to construct the psychological motivation for effective exploration that over time generates learned skills. This sensitivity to opportunities for social learning and the motivation to realize these opportunities may have underlain the evolution of our uniquely derived skill transmission system and our cultural intelligence (20, 21).

Here, we ask how this system evolved. As a first step, we can investigate what factors foster the development of exploratory tendency in our closest living relatives, the great apes. Recent studies underscore the similarity in skill development between great apes and humans, in that immatures critically rely on prolonged socially induced practice to acquire their extensive sets of learned skills (7, 8, 22–24). Maturing individuals acquire the full skill set of the local population in this way (8, 22), and studies also show that more social inputs are correlated with the acquisition of larger skill repertoires (25–27). However, despite these important similarities to the process seen in humans, there are also some differences, in particular, the presence of explicit teaching in humans and its virtual absence in apes (28). What remains unclear, then, is what drives nonsocially induced, i.e., independent, exploration of the environment in great apes, which is an important component of human curiosity.

The aim of the present study, therefore, was to investigate the link between social inputs (opportunities for social learning provided by

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association with experienced and tolerant conspecifics) and exploratory tendency in wild orangutans. Specifically, we test the hypothesis that early social inputs instill an exploratory drive in the maturing individual.

We base this test on natural variability between and within populations in orangutan sociability levels, which set the social inputs. In some populations, mother-infant pairs are on their own for up to 85% of their time, whereas, in others, they spend more than 50% of their time in association with others (29). The low mean and high variance in sociability, as well as the species' slow development, make it possible to tease apart the effects of different social factors on cognitive development. Immature orangutans virtually learn all their skills under social influence (8). Whereas the mother is an infant's sole role model in the first years of life, older infants are increasingly attracted to individuals other than the mother and, by the time they become independent juveniles, focus exclusively on them, suggesting that inputs from role models other than the mother are essential for skill development (8). During the period in which immature orangutans acquire their skills, bouts of intensive, selective social attention immediately induce practice and exploration. Accordingly, infant orangutans show a high rate of socially induced exploration (30, 31). Initial exploration rates are extremely low, steeply increase in age to a peak during mid-infancy, and then gradually drop to near-zero values around early adulthood (30, 31).

Adults and juveniles in a highly sociable orangutan population have been found to be more exploratory than individuals in a less sociable population even when alone (31). Although these findings support the notion that growing up in a more sociable population affects exploratory tendency, three uncertainties remain. First, the increased exploratory tendency of the more sociable population could also be explained by a genetic predisposition of the animals of the more sociable population to be more exploratory. Second, it remains unclear to what extent the sociability effect is indeed organizational (i.e., has long-lasting developmental effects) as opposed to merely activational (i.e., directly stimulating activity). Third, although broad differences in levels of sociability between populations may have an effect on the development of exploratory tendency, it remains unclear whether this effect also works on a more fine-grained level within populations. The exploratory tendencies of immature orangutans could, therefore, be explained by three, mutually nonexclusive factors: (i) immediate, activating factors such as the effect of food abundance on body condition or immediate social stimulation (i.e., social facilitation); (ii) developmental, organizational effects; and (iii) genetic predispositions. We develop predictions for each of them.

As for the immediate environmental effects, we would predict that (i) exploratory behavior by immatures is driven entirely by their energy balance: healthier, better nourished infants in better condition are more likely to explore their environment (32). We thus tested for the effects of food availability on exploratory tendency. An environmental model also predicts that an infant's condition will be affected by the mother's health and condition, proxies for which are her age and/or dominance.

Orangutans are ideal to test for social effects because levels of sociability vary not only across populations but also between individuals of the same population and within individuals over time. As for immediate social effects, on the basis of our previous findings (31) and findings in other species (33, 34), we predict that (ii) during all stages of development, an individual's exploratory tendency will be positively correlated with current sociability. As for the developmental

effects, patterns observed in humans lead us to predict that opportunities for social learning during development will affect orangutan exploratory tendency cumulatively and thus that (iii) an immature's exploratory tendency will be positively correlated with its overall past experienced sociability (as a measure of opportunities for social learning).

If genetic effects on exploration predominate, we expect that (iv) the immature's exploratory tendency is correlated with the exploratory tendency of its mother. Genetic effects also predict that matriline membership will explain some of the interindividual differences in exploratory tendency.

METHODS

The study was conducted over the course of 8 years at the Suaq Balimbing research site (35) in South Aceh, Indonesia and the Tuanan research site (36) in Central Kalimantan, Indonesia. Data were collected during nest-to-nest focal animal follows on immature orangutans and their mothers: 12 immatures (aged 0.5 to 13.1 years; mean, 6.5 years) and 7 mothers at Suaq and 8 immatures (aged 0.4 to 11.3 years; mean, 5.8 years) and 6 mothers at Tuanan. We differentiated between two classes of immatures: dependent immatures, which are still in permanent association with their mothers (dependency period, 0 to around 10 years at Suaq and around 8.5 years at Tuanan), and independent immatures, which are no longer in permanent association with their mothers (defined as starting from the point of time at which the offspring had spent more than two consecutive full days away from the mother) but are not yet adults (29).

Exploration was defined as prolonged, nonrepetitive, usually destructive manipulation of, or feeding attempts on, objects (such as fruits, sticks, leaves, other plant material, animal products, etc.), excluding actual or subsequent ingestion, during which the individual's visual and tactile focus is on the object (37). Exploration data were collected using all-occurrence sampling by C.S. and eight additional, highly experienced observers, whereby each exploration event was described in detail. Interobserver reliability was assessed separately for different age classes of immatures (young infants, 0 to 6 years; old infants, 6.1 to weaning age; juveniles, weaning age to adulthood). All observers surpassed 90% interobserver reliability on occurrence rates and nature of the described exploration events for the specific age classes on which their data were used.

Each age-individual exploration rate was based on individual focal data collected over a period of up to 5 months to obtain at least 40 (40 to 111; mean, 63) follow hours per data point (see table S2 for details). This amount of data was needed to reach stable values (i.e., average exploration rates remain stable with increasing number of follow hours). Each individual immature contributed to one to four "age-individual data points," producing a mixed longitudinal cross-sectional dataset. The total sample contained 40 of these data points (28 from Suaq and 12 from Tuanan), for a total of 3103 exploration events.

Sociability levels were based on 11 and 13 years of long-term focal data including association compositions assessed at 2-min intervals at Suaq and Tuanan, respectively. As a measure of sociability, we used the average number of daily association partners [including all age-sex classes, except the own mother during the dependency period (see above)], where associations were defined as being within 50 m of another individual. In a subset of detailed association data, we found this measure to be strongly correlated with the time spent in

association and the time spent in close proximity (see the Supplementary Materials). We used two different measures of sociability: (i) past experienced sociability (“past sociability”) measured as the average number of past association partners from birth until the point of data collection and (ii) currently experienced sociability (“current sociability”), defined as the average number of association partners, averaged over the current data collection period for the specific data point. Average past sociability varied between and within individuals of the same population over time and ranged from 0.58 to 2.00 (mean, 1.45) daily association partners at Suaq and 0.56 to 1.29 (mean, 0.97) at Tuanan. Similarly, average current sociability ranged from 0.36 to 3.83 (mean, 1.74) daily association partners at Suaq and 0 to 2.75 (mean, 0.87) average association partners at Tuanan. Current and past sociabilities were not significantly correlated ($r = +0.41$, $n = 40$, $P = 0.24$), allowing for multivariate analyses. Definitions of all other variables (food availability, dominance, maternal age, and matriline) and further details are provided in the Supplementary Materials.

Statistical analyses and graphs

All statistical analyses and graphs were performed using the R programming language (38). Since exploration rates showed a strong dependence on age and site, proper comparisons required correcting for these two factors. At both sites, exploration rates showed a nonlinear and highly similar age trajectory but with the Suaq rates for dependent immatures being consistently higher than at Tuanan (see fig. S1A). At the same time, several of our predictor variables showed a site effect in the same direction. However, in this study, we wanted to assess the effects of our predictor variables within each population, independent of this overall site difference. We, therefore, z -transformed the exploration rates at both sites to be able to fit the nonlinear age effect onto the complete sample (containing all data points) to maximize the resolution of this effect. We used a nonlinear least squares regression to fit the age effect on exploration rates using the *nls* functions, as implemented in the “stats” package in R (see fig. S1B and the Supplementary Materials for details). We then analyzed the effects of the predictor variables using linear mixed-effects models with z -transformed exploration rate as the response variable, age as a nonlinear effect (as described above), and individual as random factor to account for the fact that many individuals were sampled at multiple ages and thus occur multiple times in the dataset. We also z -transformed all the predictor variables that showed between site differences, namely, the two different measures of sociability, the mothers’ exploratory tendency, and food availability. All predictor variables except matriline were included as continuous variables in the models. Matriline was included as a categorical variable using Helmerts con-

trasts, as implemented in the *stats* package in R. All model fits were examined visually to assess whether they satisfied model assumptions and to check for the presence of influential observations (39).

As an alternative approach to the z transformation, we fitted the age effect on exploration rates while also including site as a factor in the initial nonlinear model (see fig. S2). This did not notably change any of the results (see the Supplementary Materials for detailed statistics). However, on the basis of the current data availability, we decided to present the z transformation approach here because it made it possible to fit the age effect using a larger sample.

We used forward model selection to assess the significance of the effects by comparing each model before and after the inclusion of each factor using the likelihood ratio test (40), in the order of our predictions. To investigate potential order effects or inflation of type I errors, we also analyzed the full model including all predictors using the *cftest* function implemented in the *multcomp* package in R.

To illustrate the effect of the different predictor variables on exploratory tendency, we showed residual plots of the linear mixed-effects models with z -transformed exploration rates, corrected for age. Throughout our analyses, we found no evidence for the effects of sex of the immatures.

RESULTS

Prediction 1: The immatures’ exploratory behavior is driven entirely by their energy balance and thus dependent on food availability

When comparing the models with and without the factor food availability using the likelihood ratio test, we found that the data do not warrant the inclusion of food availability as a factor in the model (likelihood ratio test, $P = 0.913$, $n_{\text{data points}} = 39$). We also tested for the effects of the mother’s dominance rank and age, but the data did not warrant the inclusion of either factor (likelihood ratio test, $P_{\text{Dominance}} = 0.183$, $n_{\text{data points}} = 38$; $P_{\text{Age}} = 0.417$, $n_{\text{data points}} = 40$). Thus, we found no evidence that any of the factors used to approximate an immature’s physical condition has an effect on their exploratory tendency.

Prediction 2: During all stages of development, current sociability will be positively correlated with an immature’s exploratory tendency

Model comparison showed that the data did not warrant the inclusion of the factor current sociability ($P = 0.758$, $n_{\text{data points}} = 40$) as a factor in the model. Thus, there is no evidence that current sociability levels have an effect on an immature’s current exploratory tendency.

Table 1. Effects on immature exploratory tendency (model selection approach). Model selection of individual factors using the likelihood ratio test significantly supported the inclusion of the factor past sociability as a predictor of exploration rate. Age was included as a nonlinear control variable and the individual as a random effect.

Factor	Factor type	Estimate	SE	Confidence intervals	
				0.025	0.975
Intercept	Intercept	−0.01	0.06	−0.13	0.11
function(Age)	Control	1.01	0.05	0.92	1.09
Individual	Random	—	—	—	—
Past sociability	Predictor	0.17	0.04	0.08	0.25

Prediction 3: An immature's past sociability will be positively correlated with overall exploratory tendency

Model comparison showed that the data strongly support the inclusion of the past sociability as a factor in the model (likelihood ratio test, $P < 0.001$; lmer, estimate = 0.17, $n_{\text{data points}} = 40$; Fig. 1 and Table 1). This suggests that the past experienced sociability levels have a significant positive effect on an immature's current exploratory tendency.

Prediction 4: If genetic effects on exploration predominate, then an immature's exploratory tendency will be positively correlated with that of its mother. In addition, the matriline or the identity of the mother of the immature should explain some of the interindividual differences in exploratory tendency

Model comparison showed that the data did not support the inclusion of the mother's own exploratory tendency as a factor in the model

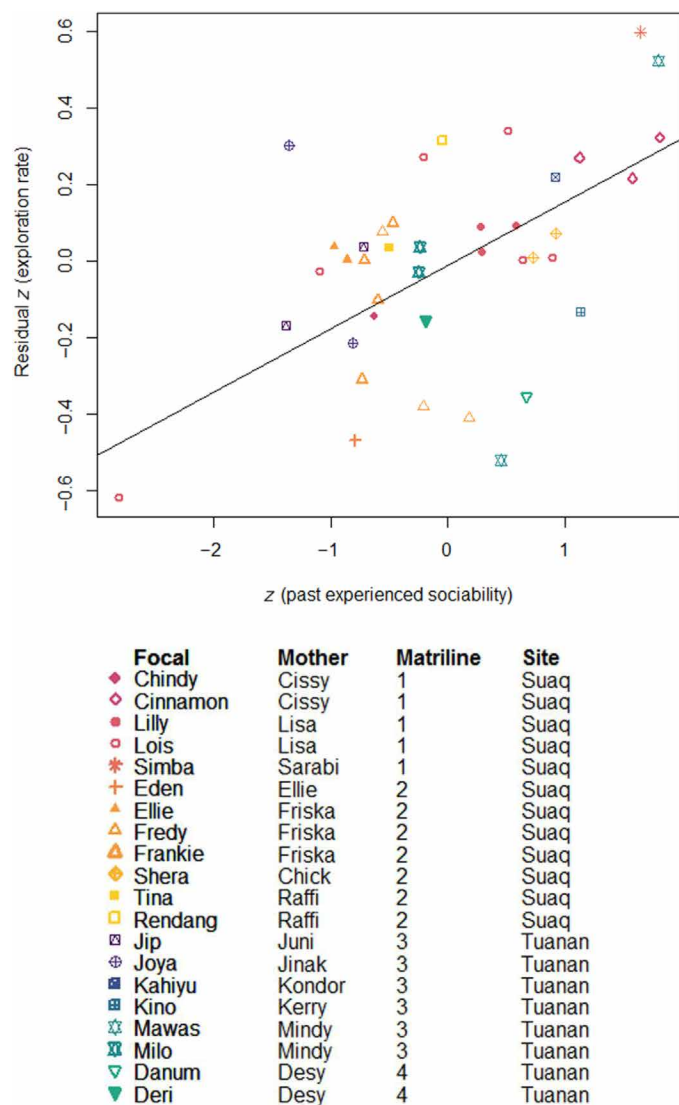


Fig. 1. Exploratory tendency as a function of past sociability. Exploratory tendency (z-transformed hourly exploration rates, corrected for age) as a function of past experienced sociability.

(likelihood ratio test, $P = 0.909$, $n_{\text{data points}} = 38$). Furthermore, there was no support for the inclusion of the matriline in the model (likelihood ratio test, $P_{\text{Matriline}} = 0.107$, $n_{\text{data points}} = 40$).

However, there was a significant difference in the raw (non-z-transformed) exploration rates between the two sites. These differences persisted when controlling for differences in experienced sociability. It is therefore very likely that the site differences in exploratory tendency are also affected by genetic predispositions [non linear least-squares regression (NLS), $P_{\text{Site K}} < 0.001$, estimate_{Site K} = 3.95; see the Supplementary Materials for details]. To avoid potential order effects or inflation of type I errors, we also analyzed the full statistical model including all tested factors, which resulted in the same results as the model selection approach (Table 2).

DISCUSSION

We analyzed the effects of different factors on exploratory tendency in wild immature orangutans. We found no evidence for effects of food availability, the mother's age, or her dominance status on exploratory tendency. However, both sites have the highest-known orangutan density on Sumatra and Borneo, respectively (41), suggesting a high level of food availability for orangutan habitats. The absence of any effects of food availability on exploration rates at Suaq and Tuanan, therefore, does not rule out that these effects may be present at other times or places where food availability falls below a critical threshold and then affects body condition and thus energy levels of individuals. Even so, the present study does not support the idea that ecological pressure ("necessity") within the range studied increases rates of exploration and thus the probability of innovations.

In terms of social factors, we found no effect of the level of current sociability on immature exploratory tendency. At first sight, this might indicate that infant orangutans get distracted by social stimuli (e.g., social play with infant association partners), which might cancel out any positive effects of a greater number of role models on exploration. However, in an earlier study, we found that associations positively affected adult and juvenile orangutans' exploratory tendency (31), presumably because they allow an individual to direct its attention to an object, while the association partner remains vigilant for potential surrounding threats [vigilance effect (33)]. The lack of such a positive effect on infants may reflect the fact that unlike adults and juveniles, infant orangutans are always in association with their mothers. This may provide them with enough time and energy to engage in exploration and presumably other energy-consuming activities with no immediate function, whereas the presence of additional association partners does not have an additional effect. Accordingly, exploration rates of immatures drop around the onset of juvenility when the permanent association with the mother ends.

We found strong evidence that the past experienced sociability is a significant predictor of an immature's exploratory tendency. Given that exploratory tendency has previously been shown to be a measure of problem-solving ability and thus cognitive ability (10, 12), our results suggest that in orangutans, opportunities for social learning during development are important for cognitive development. This is consistent with the finding that children growing up with an increased frequency and quality of social inputs during early development later show increased exploratory behavior and cognitive performance (12, 19). It is also consistent with the finding that with increasing levels of enculturation, rehabilitant orangutans are more exploratory (42). Exploratory tendency has been shown to be an

Table 2. Effects on immature exploratory tendency (full model). The analysis of the full model, containing all tested factors as predictor variables on exploration rate, as well as age as a nonlinear control variable and the individual as a random effect.

Factor	Factor type	Estimate	SE	Confidence intervals		P value (cf test)
				0.025	0.975	
Intercept	Intercept	−0.31	0.33	−0.79	0.23	0.348
function(Age)	Control	1.01	0.07	0.91	1.13	<0.001
Fruit availability	Predictor	0.01	0.05	−0.08	0.09	0.862
Mothers dominance	Predictor	0.15	0.12	−0.06	0.33	0.222
Mothers age	Predictor	−0.02	0.11	−0.20	0.14	0.828
Current sociability	Predictor	−0.08	0.05	−0.17	0.01	0.159
Past sociability	Predictor	0.20	0.06	0.11	0.29	<0.001
Mother's exploratory tendency	Predictor	−0.10	0.07	−0.20	0.01	0.130
Matriline	Predictor	*	*	*	*	*
Individual	Random	—	—	—	—	—

*Matriline was included as a categorical variable, whereby none of the contrasts showed a significant difference.

important determinant of problem-solving success (10–12) and innovation probability (13, 43). Accordingly, we would expect that orangutans with a greater exploratory tendency as immatures will later generate more innovations, leading to larger repertoires of learned skills as adults. Following our immature study, animals into adulthood would allow this prediction to be tested.

It would be very interesting to see which kind of associations have the strongest effect on orangutan cognitive development. It may well be that stressful associations (e.g., mating consortships during which a male guards a female to prevent her from mating with other males) have no or even the opposite effect on the development of exploratory tendency, whereas voluntary associations have the strongest positive effects. It may also be that as in humans (44), there are specific time windows throughout development during which these effects are strongest. Pinpointing the importance of the type and timing of the associations will also allow us to investigate the mechanisms that underlie this phenomenon in more detail. In humans, it has been suggested that infants use others' reactions to guide their own behavior in selective ways, depending on the characteristics of the role model and across different contexts, a process called social referencing. In combination with results on social learning, the results of the current study may in the future shed light on whether similar processes are at work in wild orangutans. Increasing our dataset over the coming years will allow for these more detailed analyses.

In terms of genetic effects, the overall differences in exploration rates between the two study populations Suaq and Tuanan found here offer support for innate population differences in exploratory tendency. However, since the two sites also differ in their level of sociability and social tolerance (31), the site difference in exploration rates we observed in this study may also reflect differences in sociability experienced during development. To explore baseline differences in exploration rates corrected for sociability, a larger dataset will be needed.

Although there is evidence for heritable innate predispositions of exploratory tendency in orangutans at the species level (45), we found no evidence for more fine-grained genetic influences, including

no effect of the mother's own exploratory tendency on her offspring's exploratory tendency. Our results suggest that opportunities for social learning provided by a larger number of different role models are the major influence on subsequent exploration rates, which is consistent with what has been shown experimentally in humans (46). In a previous study, we could show that around age 3, when orangutan infants have already acquired a basic skill set and some understanding of most skills, they show a steep increase in interest in role models other than the mother (8). In combination with the current findings, this suggests that social effects become most prominent during late infancy.

The orangutan pattern contrasts with human studies, showing that genetic influences account for 40 to 80% of the variance in intellectual performance (16). The magnitude of genetic effects on intelligence, however, depends on the variance in the sample (47), thus, in the case of this study, the variance of both genetic background and social inputs. In humans, heritability in intelligence has been shown to be highly age dependent (48), which strongly suggests that we increasingly select the quantity and quality of social inputs as we become independent (49). In orangutans, ecological conditions (e.g., limited food availability) will generally prevent them from forming extensive associations once they become an adult, leading to a stronger "shared environment" effect and a weaker impact of genetic factors.

In conclusion, the social environment plays a key role in the developmental construction of cognitive abilities in both orangutans and humans, suggesting that this process has deep roots, going back at least to the common ancestors of all great apes. Specifically, they reveal a shared model of cognitive development in which social inputs can up-regulate the baseline level of exploration set by natural selection, because they allow the maturing individual to refine its assessment of nondangerous opportunities for exploration, and thus elicit an appropriate level of curiosity. These findings, therefore, support the cultural intelligence hypothesis (20) [see also (10, 27, 50)], which also predicts that over evolutionary time, increased opportunities for social learning select for increased innate learning ability (45, 51), as arguably happened in human evolution (21, 52).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/2/eaaw2685/DC1>

Section S1. Details on the predictor variables

Section S2. Details on the statistical analyses presented in the main manuscript

Section S3. Alternative statistical approach

Fig. S1. Exploration rates over age.

Fig. S2. Exploratory tendency (number of exploration events per hour) as a function of age for Suaq and Tuanan.

Table S1. Effects on immature exploratory tendency (full model).

Table S2. Data used for all analyses in the main text and the Supplementary Materials.

References (53–56)

[View/request a protocol for this paper from Bio-protocol.](#)

REFERENCES AND NOTES

- S. M. Reader, Y. Hager, K. N. Laland, The evolution of primate general and cultural intelligence. *Philos. Trans. R. Soc., B* **366**, 1017–1027 (2011).
- C. Ross, K. E. Jones, Socioecology and the evolution of primate reproductive rates, in *Comparative Primate Socioecology*, P. Lee, Eds. (Cambridge Studies in Biological Anthropology, Cambridge Univ. Press, 1999), vol. 22, pp. 73–110.
- C. Schuppli, K. Isler, C. P. van Schaik, How to explain the unusually late age at skill competence among humans. *J. Hum. Evol.* **63**, 843–850 (2012).
- S. R. Quartz, T. J. Sejnowski, The neural basis of cognitive development: A constructivist manifesto. *Behav. Brain Sci.* **20**, 537–556 (1997).
- C. Heyes, Social learning in animals: Categories and mechanisms. *Biol. Rev.* **69**, 207–231 (1994).
- B. G. Galef, Laboratory studies of imitation/field studies of tradition: Towards a synthesis in animal social learning. *Behav. Processes* **112**, 114–119 (2015).
- A. Whiten, Experimental studies illuminate the cultural transmission of percussive technologies in Homo and Pan. *Philos. Trans. R. Soc., B* **370**, 20140359 (2015).
- C. Schuppli, E. J. M. Meulman, S. I. F. Forss, F. Aprilinayati, M. A. van Noordwijk, C. P. van Schaik, Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Anim. Behav.* **119**, 87–98 (2016).
- S. M. Reader, K. N. Laland, Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl. Acad. Sci. U.S.A.* **99**, 4436–4441 (2002).
- L. A. Damerius, S. I. F. Forss, Z. K. Kosonen, E. P. Willems, J. M. Burkart, J. Call, B. M. F. Galdikas, K. Liebal, D. B. M. Haun, C. P. van Schaik, Orientation toward humans predicts cognitive performance in orang-utans. *Sci. Rep.* **7**, 40052 (2017).
- S. Benson-Amram, K. E. Holekamp, Innovative problem solving by wild spotted hyenas. *Proc. R. Soc. B* **279**, 4087–4095 (2012).
- D. A. Caruso, Dimensions of quality in infants' exploratory behavior: Relationships to problem-solving ability. *Infant Behav. Dev.* **16**, 441–454 (1993).
- S. E. Overington, L. Cauchard, K.-A. Côté, L. Lefebvre, Innovative foraging behaviour in birds: What characterizes an innovator? *Behav. Processes* **87**, 274–285 (2011).
- P. Schuetze, A. Lewis, D. DiMartino, Relation between time spent in daycare and exploratory behaviors in 9-month-old infants. *Infant Behav. Dev.* **22**, 267–276 (1999).
- J. Chappell, N. Cutting, E. C. Tecwyn, I. A. Apperly, S. R. Beck, S. K. S. Thorpe, Minding the gap: A comparative approach to studying the development of innovation, in *Animal creativity and innovation* (Elsevier, 2015), pp. 287–316.
- R. Plomin, F. M. Spinath, Intelligence: Genetics, genes, and genomics. *J. Pers. Soc. Psychol.* **86**, 112–129 (2004).
- C. A. Nelson III, C. H. Zeanah, N. A. Fox, P. J. Marshall, A. T. Smyke, D. Guthrie, Cognitive recovery in socially deprived young children: The bucharest early intervention project. *Science* **318**, 1937–1940 (2007).
- T. J. Eluvathingal, H. T. Chugani, M. E. Behen, C. Juhász, O. Muzik, M. Maqbool, D. C. Chugani, M. Makki, Abnormal brain connectivity in children after early severe socioemotional deprivation: A diffusion tensor imaging study. *Pediatrics* **117**, 2093–2100 (2006).
- S. Maggi, L. J. Irwin, A. Siddiqi, C. Hertzman, The social determinants of early child development: An overview. *J. Paediatr. Child Health* **46**, 627–635 (2010).
- E. Herrmann, J. Call, M. V. Hernández-Lloreda, B. Hare, M. Tomasello, Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science* **317**, 1360–1366 (2007).
- A. Whiten, C. P. van Schaik, The evolution of animal 'cultures' and social intelligence. *Philos. Trans. R. Soc., B* **362**, 603–620 (2007).
- E. Lonsdorf, What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (Pan troglodytes schweinfurthii)? *Anim. Cogn.* **9**, 36–46 (2006).
- C. Schuppli, S. I. F. Forss, E. J. M. Meulman, N. Zweifel, K. C. Lee, E. Rukmana, E. R. Vogel, M. A. van Noordwijk, C. P. van Schaik, Development of foraging skills in two orangutan populations: Needing to learn or needing to grow? *Front. Zool.* **13**, 43 (2016).
- T. Matsuzawa, D. Biro, T. Humle, N. Inoue-Nakamura, R. Tonooka, G. Yamakoshi, Emergence of culture in wild chimpanzees: Education by master-apprenticeship, in *Primate Origins of Human Cognition and Behavior*, T. Matsuzawa, Eds. (Springer, 2001), pp. 557–574.
- K. A. Bard, K. H. Gardner, Influences on development in infant chimpanzees: Enculturation, temperament, and cognition, in *Reaching into Thought: The Mind of Great Apes*, A. Russon, K. Bard, S. T. Parker, Eds. (Cambridge Univ. Press, 1996), pp. 235–255.
- J. Call, M. Tomasello, The effects of humans on the cognitive development of apes, in *Reaching into Thought: The Minds of the Great Apes*, A. E. Russon, K. A. Bard, S. T. Parker, Eds. (Cambridge Univ. Press, 1996), pp. 371–403.
- S. Savage-Rumbaugh, W. M. Fields, P. Segerdahl, D. Rumbaugh, Culture prefigures cognition in Pan/Homo bonobos. *Theoria. Revista de Teoría, Historia y Fundamentos de la Ciencia* **20**, 311–328 (2005).
- G. Gergely, G. Csibra, Natural pedagogy, in *Navigating the Social World: What Infants, Children, and Other Species Can Teach Us*, M. R. Banaji, S. A. Gelman, Eds. (Oxford Univ. Press, 2013), pp. 127–132.
- M. A. Van Noordwijk, S. E. B. Sauren, Nuzuar, A. Abulani, H. C. Morrogh-Bernard, S. S. Utami Atmoko, C. P. van Schaik, Developmental of independence. Sumatran and Bornean orangutan compared, in *Orangutans Compared: Geographic Variation in Behavioral Ecology and Conservation*, S. A. Wich, T. Mitra Setia, S. A. Utami Atmoko, C. P. van Schaik, Eds. (Oxford Univ. Press, 2009), pp. 189–203.
- C. P. van Schaik, J. Burkart, L. Damerius, S. I. F. Forss, K. Kooops, M. A. van Noordwijk, C. Schuppli, The reluctant innovator: Orangutans and the phylogeny of creativity. *Philos. Trans. R. Soc., B* **371**, 20150183 (2016).
- C. Schuppli, S. Forss, E. Meulman, S. U. Atmoko, M. van Noordwijk, C. van Schaik, The effects of sociability on exploratory tendency and innovation repertoires in wild Sumatran and Bornean orangutans. *Sci. Rep.* **7**, 15464 (2017).
- H. Kummer, J. Goodall, Conditions of innovative behaviour in primates. *Philos. Trans. R. Soc. B* **308**, 203–214 (1985).
- G. Roberts, Why individual vigilance declines as group size increases. *Anim. Behav.* **51**, 1077–1086 (1996).
- E. Addessi, F. Chiarotti, E. Visalberghi, A. A. Anzenberger, Response to novel food and the role of social influences in common marmosets (*Callithrix jacchus*) and Goeldi's monkeys (*Callimico goeldii*). *Am. J. Primatol.* **69**, 1210–1222 (2007).
- C. P. van Schaik, The socioecology of fission-fusion sociality in orangutans. *Primates* **40**, 69–86 (1999).
- C. P. van Schaik, S. A. Wich, S. S. Utami, K. Odum, A simple alternative to line transects of nests for estimating orangutan densities. *Primates* **46**, 249–254 (2005).
- T. G. Power, *Play and Exploration in Children and Animals* (Lawrence Erlbaum Associates, 2000).
- R Development Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2015).
- F. E. Harrell Jr., *Regression Modeling Strategies: With Applications to Linear Models, Logistic and Ordinal Regression, and Survival Analysis* (Springer, 2015).
- J. Fox, *Applied Regression Analysis and Generalized Linear Models* (Sage Publications, 2015).
- S. J. Husson, S. A. Wich, A. J. Marshall, R. D. Dennis, M. Ancrenaz, R. Brassey, M. Gumal, A. J. Hearn, E. Meijaard, T. Simorangkir, I. Singleton, Orangutan distribution, density, abundance and impact of disturbance, in *Orangutans Geographic Variation in Behavioral Ecology and Conservation*, S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, C. P. van Schaik, Eds. (Oxford Univ. Press, 2009), pp. 78–96.
- L. A. Damerius, S. M. Graber, E. P. Willems, C. P. van Schaik, Curiosity boosts orang-utan problem-solving ability. *Anim. Behav.* **134**, 57–70 (2017).
- S. M. Reader, Innovation and social learning: Individual variation and brain evolution. *Anim. Biol.* **53**, 147–158 (2003).
- C. Rovee-Collier, Time windows in cognitive development. *Dev. Psychol.* **31**, 147–169 (1995).
- S. I. Forss, E. Willems, J. Call, C. P. van Schaik, Cognitive differences between orang-utan species: A test of the cultural intelligence hypothesis. *Sci. Rep.* **6**, 30516 (2016).
- M. Muthukrishna, B. W. Shulman, V. Vasilescu, J. Henrich, Sociality influences cultural complexity. *Proc. R. Soc. B* **281**, 20132511 (2014).
- R. E. Nisbett, J. Aronson, C. Blair, W. Dickens, J. Flynn, D. F. Halpern, E. Turkheimer, Intelligence: New findings and theoretical developments. *Am. Psychol.* **67**, 130–159 (2012).
- M. McGue, T. J. Bouchard Jr, W. G. Iacono, D. T. Lykken, Behavioral genetics of cognitive ability: A life-span perspective, in *Nature, Nurture, and Psychology*, R. Plomin, G. E. McClearn, Eds. (American Psychological Association, 1993), pp. 59–76.
- J. R. Flynn, *Does Your Family Make You Smarter?: Nature, Nurture, And Human Autonomy* (Cambridge Univ. Press, 2016).
- K. A. Bard, R. Bakeman, S. T. Boysen, D. A. Leavens, Emotional engagements predict and enhance social cognition in young chimpanzees. *Dev. Sci.* **17**, 682–696 (2014).

51. A. Whiten, Culture extends the scope of evolutionary biology in the great apes. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 7790–7797 (2017).
52. K. N. Laland, *Darwin's Unfinished Symphony: How Culture Made The Human Mind* (Princeton Univ. Press, 2018).
53. A. J. Marshall, R. Lacy, M. Ancrenaz, O. Byers, S. J. Husson, M. Leighton, E. Meijaard, N. Rosen, I. Singleton, S. Stephens, K. Traylor-Holzer, S. S. Utami Atmoko, C. P. van Schaik, S. A. Wich, Orangutan population biology, life history, and conservation, in *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*, S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, C. P. van Schaik, Eds. (Oxford Univ. Press, 2009), pp. 311–326.
54. M. A. van Noordwijk, S. S. Utami Atmoko, C. D. Knott, N. Kuze, H. C. Morrogh-Bernard, F. Oram, C. Schuppli, C. P. van Schaik, E. P. Willems, The slow ape: High infant survival and long interbirth intervals in wild orangutans. *J. Hum. Evol.* **125**, 38–49 (2018).
55. I. Lenzi, thesis, University of Zürich (2014).
56. N. Arora, M. A. Van Noordwijk, C. Ackermann, E. P. Willems, A. Nater, M. Greminger, P. Nietlisbach, L. P. Dunkel, S. S. U. Atmoko, J. Pamungkas, D. Perwitasari-Farajallah, C. P. Van Schaik, M. Krützen, Parentage-based pedigree reconstruction reveals female matrilineal clusters and male-biased dispersal in nongregarious Asian great apes, the Bornean orang-utans (*Pongo pygmaeus*). *Mol. Ecol.* **21**, 3352–3362 (2012).

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