Eight years of social and asocial learning synergistically shape orangutan diet profiles

*T Revathe[1], Marie-Theres Weidling[1], Sri Suci Utami-Atmoko[2,3], Tatang Mitra Setia[4], Imran Razik[5], Carel P. van Schaik[6,7], Andrew Whiten[8], Paul-Christian Bürkner[9], *Caroline Schuppli[1,7]

[1]Development and Evolution of Cognition Research Group, Max Planck Institute of Animal Behavior, Konstanz, Germany

[2]Department of Biology, Graduate Program, Faculty of Biology and Agriculture, Universitas Nasional, Jalan Sawo Manila, Jakarta, Indonesia

[3]Primate Research Center, Universitas Nasional, Jalan Sawo Manila, Jakarta, Indonesia

[4]Fakultas Biologi, Universitas Nasional, Jalan Sawo Manila, Jakarta, Indonesia

[5]Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, Germany

[6]Comparative Socioecology Group, Max Planck Institute of Animal Behavior, Konstanz, Germany

[7]Department of Evolutionary Anthropology, University of Zurich, Zurich, Switzerland

[8]Centre for Social Learning and Cognitive Evolution, School of Psychology and Neuroscience, University of St Andrews, St Andrews, UK

[9]Department of Statistics, TU Dortmund University, Dortmund, Germany

ORCID T.R., 0000-0003-2471-9194; S.S.U-A., 0000-0001-5550-8344; T.M.S., 0000-0003-2667-5199; I.R., 0000-0002-8529-6212; C.P.v.S, 0000-0001-5738-4509; A.W., 0000-0003-2426-5890; P.B., 0000-0001-5765-8995; C.S., 0000-0001-6318-2815

Correspondence and requests for materials should be directed to T Revathe (rthillaikumar@ab.mpg.de) or Caroline Schuppli (cschuppli@ab.mpg.de)

Abstract

The adult competences that underlie humanity's global dominance are massively dependent on learning from one's culture across many years of childhood[1,2]. Recent research has demonstrated cultural learning in a growing diversity of species[3,4], but has largely been studied through mere snapshots of animals' lives and specific behavioural achievements like tool use[5,6]. Thus, how different forms of learning interact to shape the full arc of individuals' behavioural development in the wild remains unknown. Here, we analyse nearly seven thousand records of behavioural indicators of social and asocial learning in wild, immature orangutans, from birth to independence at around eight years. We show that learning is largely triggered by social observation, the effect of which lasts for hours. Social learning events were five times more frequent than asocial learning events. Immatures show substantial differences in their reliance on different forms of social and asocial learning during development. We demonstrate that individuals with the highest rates in both modes of learning developed the broadest diets, and the benefits of social learning were the strongest when asocial learning was low. Extending to over 250 food items in adults, diet breadth represents a comprehensive measure of ecological competence, rather than reflecting mastery of a single behaviour. Our detailed analyses reveal that social and asocial learning synergistically shape great ape ecological competence substantially more than previously recognised. Our study marks a step-change in methodological approaches concerning both the scale of cultural and asocial learning across development and its impacts on broad-scale competences critical for later life. It offers a launching point for both the focused investigation of individual-specific learning trajectories shaping development, and the interaction between social and asocial learning in progressing toward adult-like repertoires in non-human wild animals and humans alike.

Until as recently as the middle of the last century, culture was thought to be a feature of humanity that separates our species from the remainder of the animal kingdom[7]. Recent research has revealed that to the contrary, culture defined as "information capable of affecting individuals' behaviour that they acquire from other members of their species through (…) forms of social transmission"[8], is widespread in the animal kingdom, extending to all main vertebrate taxa and even insects[3,4,9].

The evidence on which our understanding of animal culture is based, however, is very much a scientific patchwork based on a diversity of methodologies that have largely focused on short-term events in subjects' lives and on relatively specific outcomes. Examples include tracing the diffusion of innovations across social networks, either spontaneously, as in the spread of moss-sponging in wild chimpanzees[10], or experimentally seeded, as in the case of novel foraging techniques in wild great tits[11], or understanding the acquisition of specific preexisting complex behaviours, as in the case of tool use, through long-term observational studies[12–14]. There are a few exceptions, where long-term studies in the wild have investigated possible social transmission of a broad competence – diet repertoire – but the evidence is either contextual[15] or drawn only from simulations[16]. There is also a large corpus of rigorous experimental studies with captive populations, as in demonstrating the spread of challenging new tool use and other foraging techniques, from chimpanzees[17] to bumblebees[18]. Numerous such studies now point to the existence of social learning capacities and pervasive cultural transmission in animals' lives[3,4,9,17–20], but none capture the scale of what culture in the wild is thought to entail, in the round: a capacity to learn potentially very many things in the course of individuals' development, generating a corresponding breadth of competence necessary for successful adult life. This is the main target of the present study.

Of course, animals likely also learn through their own individual efforts, called asocial learning. While asocial learning is thought to be less efficient and entail greater risks than social learning (such as poisoning and predation[21]), a strict reliance on social learning can compromise individual's adaptability to changing conditions[22] and may eventually lead to repertoire erosion due to incomplete transmission[23]. A handful of studies have accordingly begun to implement statistical models of "experience-weighted attraction" (EWA), which evaluate the relative roles of social and asocial learning in the acquisition of novel tasks[6,24–27]. The learning effects investigated in these studies were relatively short term, limited to the duration of the experiment, and to a single outcome of either tool use or the spread of a feeding technique. Experimental studies provide evidence for individual differences in the use of social and asocial learning[14,28,29], but findings are mixed as to whether an individual's reliance on one learning mode predicts their reliance on the other[30–32]. A negative correlation between social and asocial learning propensities within individuals may arise from systematic differences among individuals in whether they predominantly pay attention to environmental or social cues[31], likely reflecting an underlying trade-off between investing in the two modes of learning. In contrast, a positive correlation may suggest a stimulating developmental effect of social learning on asocial learning abilities[33]. For such within-individual correlations to be

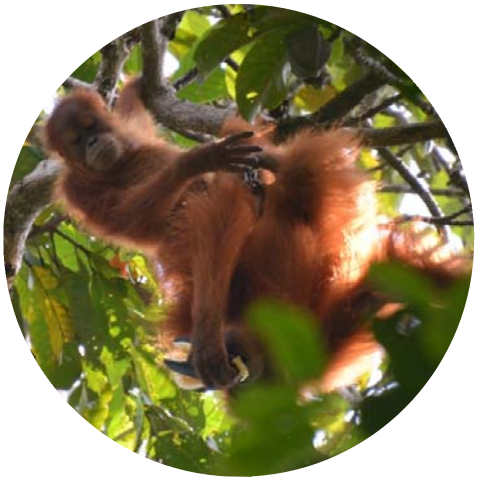
adaptive, combinations of social and asocial learning should have distinct effects on individuals' acquisition of adaptive behaviours.

To this day, our understanding of the combined effects of social learning and asocial learning, including the effects of individual variation in learning propensities on individuals' broad scale behavioural development remains minimal. By linking individual variation in social and asocial learning propensities to a behavioural outcome, we can evaluate whether there is a functional, adaptive trade-off or synergy between the two modes of learning. Accordingly, we have pursued a research programme that is significantly more expansive, in two main respects. First, we collected measures of the whole gamut of both asocial and social information-seeking events across immature orangutans' ~8.5-year dependency period (Supplementary Fig. 1); and second, we evaluated the consequence of individual variation in the occurrence of these events for a global measure of "ecological competence" indexed by the breadth of dietary profile (number of identified, distinct food items eaten) achieved at independence (Supplementary Fig. 2,3). Adult orangutan diet encompasses a challenging total of around 250 different items selected from thousands of options in the forest[16], so our outcome measure of diet breadth is a significant indicator of the foraging competence that will determine how an individual fares post-independence, with consequent implications for its lifetime fitness.

We examined over 6,700 detailed all-occurrence records of peering behaviour, as a measure of seeking information socially (Fig. 1A), and exploration behaviour, as a measure of seeking information asocially (Fig. 1B). These data were collected over 12 years of study and over 1,700 hours of detailed direct observation of 21 immature Sumatran orangutans (*Pongo abelii*) at the Suaq Balimbing research area, starting from their birth to the onset of independence. The dependency period ends at around 8.5 years of age when permanent association with the mother ceases and is the period during which most foraging competence develops[34]. Peering is defined as sustained, attentive, close-range observation of the behaviours of conspecifics[15]. The Suaq orangutans are estimated to peer for around 40,000 times over the course of their lifetime[35]. That immatures follow peering by trying to repeat what they witness strongly suggests that individuals use peering to socially acquire ecological competence, including knowing what to eat and how to process the food items, sometimes involving tool use[15,36,37]. We, therefore, used peering rate as a measure of an individual's propensity to seek information socially, indexing social learning. Exploration is a key component of asocial learning[38]. We defined object exploration as prolonged, nonrepetitive—often destructive—manipulation of objects[39]. Age trajectories of the frequency, diversity, and persistence of exploratory object manipulation behaviours suggest that the orangutans at Suaq may also learn through such behaviour[39,40]. We thus used exploration rate as a measure of an individual's propensity to seek information asocially, indexing asocial learning.

1

a Peering



b Exploration

c Dietary profile of immatures

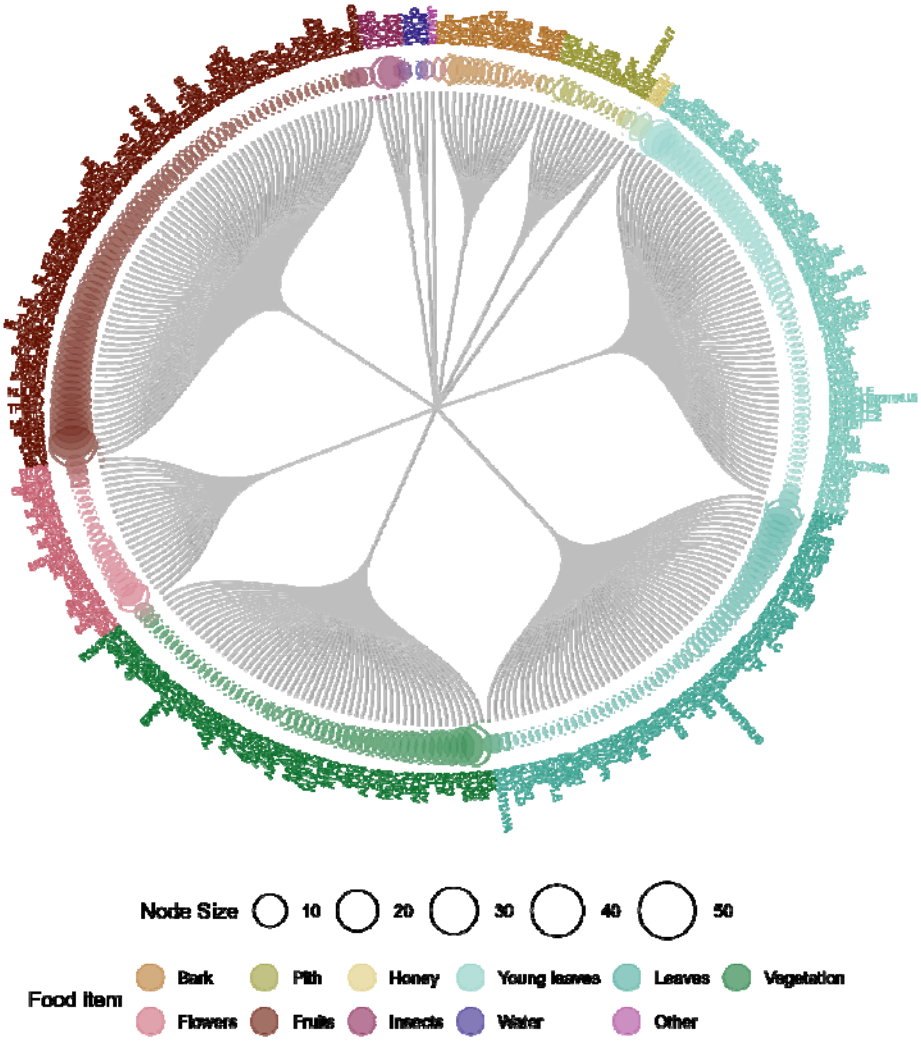


Fig. 1. A Sumatran orangutan immature a) *peering* at its mother, who is feeding on Neesia fruit and b) *exploring* a Neesia fruit using a stick tool and c) all the recorded unique food items (*N*=303) eaten by a subset of 13 focal immatures for whom we had sufficient data for analysing their ecological competence achieved at the onset of independence. Each vertex (grey line) indicates a food item. Each node (coloured circle) represents a food species. Node size represents the recorded number of times each food item was consumed by these immatures during the study period.

We hypothesized that immature orangutans engage in both asocial and social forms of learning to develop broad ecological competence. Specifically, we tested whether:

(i) Immatures engage more frequently in social or asocial learning.
(ii) Immatures show distinct individual propensities for both social and asocial learning, and these propensities are correlated at the individual level.
(iii) Immatures´ levels of social and asocial learning affect their development of ecological competence, and the effect of one learning mode depends on the level of engagement in the other.

Peering is more frequent than exploration and most exploration events are elicited by prior peering

Previous research suggests that peering elicits an immediate increase in exploration[15], which suggests that the two learning modes interact. We, therefore, conducted a hazard analysis to estimate the time point at which the instantaneous rate of exploration stabilised following a peering event, indicating a return to baseline exploration rates. We were able to incorporate an unprecedented number of peering (*N*=2113) and exploration (*N*=4649) events recorded across the 12 study years in our analysis (Supplementary Fig. 1). We used data only from immature individuals who had not yet reached independence from their mothers, meaning they were in constant association with her (*N*=21 immatures). On average, immatures peered at a rate of 1.25 events/h (SD=1.205 events/h) and explored at a rate of 3.71 events/h (SD=4.112 events/h), suggesting that they seemingly have a higher propensity to explore than peer. However, we found that most exploration events are far from truly individually initiated. We found that, in general, exploration events became independent of prior peering only at 145 minutes (Supplementary Fig. 4), highlighting a previously underexplored, intimate intertwining of social and asocial information seeking at the immediate, proximate level. We refer to the exploration events that occurred within 145 minutes of the preceding peering event and before the subsequent peering event as socially initiated explorations (SIE; *N*=4235 events) and those that occurred at or beyond 145 minutes as individually initiated explorations (IIE; *N*=414 events). Immatures individually initiated explorations at a rate of only 0.25 events/h, (SD=0.801 events/h), which was ~5 and ~6 times lower than peering and SIE rates, respectively, indicating that IIE events are relatively rare in wild orangutans (Supplementary Fig. 5).

Social and asocial information-seeking propensities are individual-specific

We analysed the total number of times immatures engaged in peering (*N*=260 focal follow days), SIE (*N*=257 focal follow days), and IIE (*N*=257 focal follow days) during each follow using three univariate Bayesian Generalised Linear Mixed effects Models (GLMM; U1, U2, and U3), controlling for immature's age, sex, daily average number of association partners, monthly food availability, and observation duration, because these factors are known to have an effect on peering and exploration[15,34,36,41,42]. We, therefore, refer to the resulting measures as the immatures' *individual* propensities for peering, SIE, and IIE, which may arise from developmental and/or genetic influences. By including the number of association partners as a control in our model, we account for differences in social learning opportunities across the focal immatures. As these immatures live in highly overlapping home ranges[43], systematic habitat-induced differences in asocial learning opportunities are not likely. We included a random intercept of immature identity to estimate social and asocial information-seeking propensities for each immature and the variation in these propensities among immatures.

We found significant variation among immatures in all three information-seeking propensities (Supplementary Table 1), suggesting that, on average, immatures differ from one another in their use of both social and asocial information-seeking opportunities. Importantly, immatures differed from one another to a lesser extent in peering rate (SD of estimated individual average peering rate [95% CI]=0.69 [0.16, 1.42]; Fig. 2a) than in SIE rate (SD of estimated individual average SIE rate [95% CI]=1.24 [0.09, 2.80]; Fig. 2b) or IIE rate (SD of estimated individual average IIE rate [95% CI]=1.05 [0.11, 2.56]; Fig. 2c).

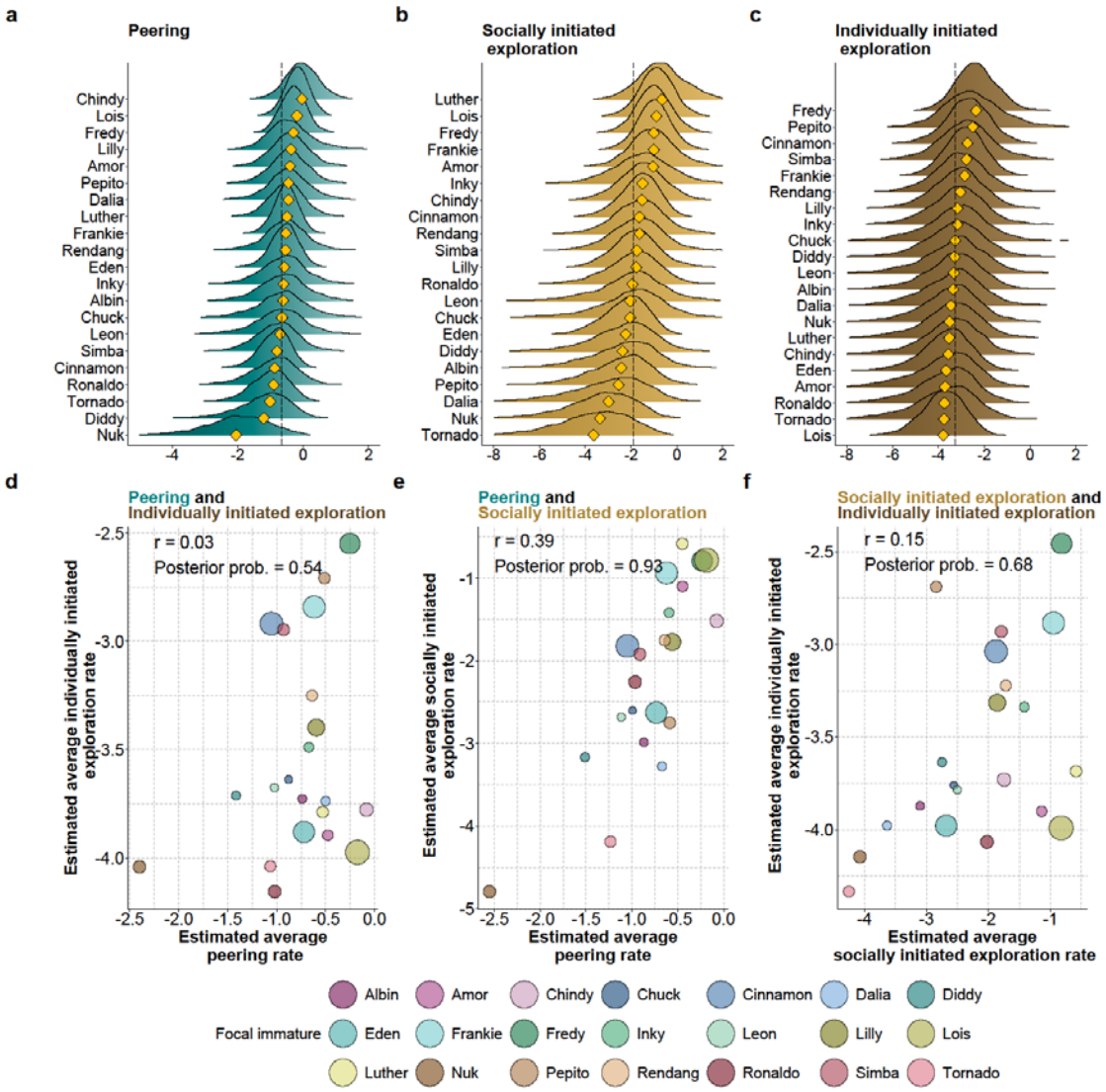


Fig. 2. Substantial individual variation in information-seeking propensities and within-individual relationships between social and asocial information-seeking propensities. Posterior distributions of the estimated average a) peering, b) socially initiated exploration, and c) individually initiated exploration rates (per hour) for 21 immatures over their 8.5-year developmental period. The dashed black line represents the average over all immatures, and the yellow diamond represents the posterior mean of the estimates for each immature. Values to the left of the dashed line represent lower, and those to the right higher, than population average peering/exploration rates. Note that the x-axis scales are different among a), b), and c). Scatterplots of individuals' posterior mean d) peering and individually initiated exploration rates, e) peering and socially initiated exploration rates, and f) socially initiated exploration rates and individually initiated exploration rates for the 21 immatures. Circle size represents the total observation duration for each immature between birth and 8.5 years of age (N = 2-360 hours). Correlation *r* and posterior probabilities for the hypothesis '*r* > 0' are shown.

Within individuals, information-seeking propensities are not correlated to each other

We fit three multivariate models: peering events and IIE events (M1), peering and SIE events (M2), and SIE events and IIE events (M3). The models showed no significant correlation between immatures' different information-seeking rates (Supplementary Table 2; Fig. 2d-f), suggesting that not all peering events trigger a similar number of SIE events and that immatures who peered at a higher rate did not necessarily individually explore at a higher rate. However, peering and total exploration rates (the sum of SIE and IIE) were significantly positively correlated (M4; Supplementary Table 2). Ignoring the effect of peering on subsequent exploration can, therefore, erroneously suggest a positive correlation between rates of social and asocial information seeking at the individual level. We then used the estimated individual peering and IIE rates from M1 as predictors of immatures' ecological competence in our critical non-linear model to predict the effects of our measures of learning during development on ecological competence at the onset of independence.

Inferring different modes of learning using long-term observations of wild individuals

We developed a new analytical approach to infer the contributions of different modes of learning to competence development in wild individuals, linking individual variation in information-seeking propensities during development to individual variation in broad-scale ecological competence at the onset of independence from the mother (Fig. 3).

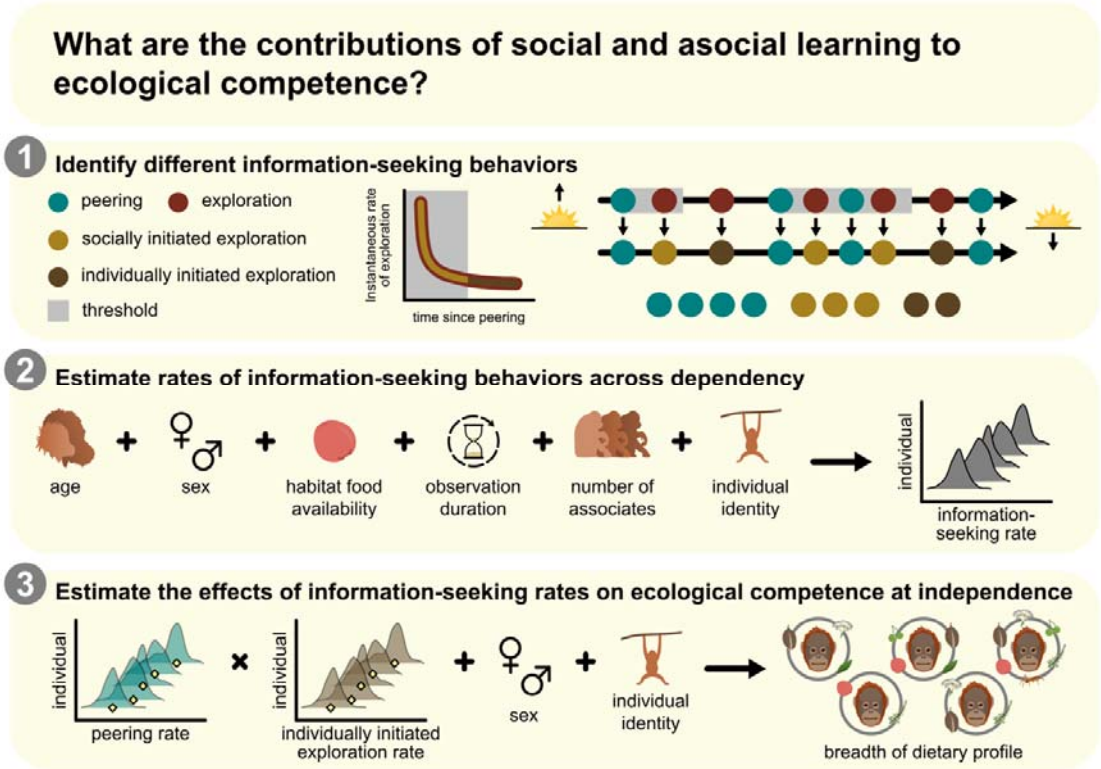


Fig. 3. Testing the effects of social (peering) and asocial (individually initiated exploration) information-seeking propensities on the development of ecological

competence. Our approach was to first identify different information-seeking behaviours shown by the immatures, followed by the estimation of the average rates of these behaviours shown by each immature during development, to finally test the effects of these rates on the breadth of individual immature's dietary profile at independence.

Recognizing food items in their forest habitats is one of the most fundamental ecological competences wild orangutans need to develop to survive, especially when they become independent of their mothers and transition to a more semi-solitary lifestyle. Immature orangutans take ~8 years (i.e., their entire dependency period) to reach the approximate breadths of the dietary profiles of their mothers[34]. Because diet profiles are composed of distinct units (i.e., food items), their development is quantifiable. We thus used the breadth of the immatures' diet profile as a measure of ecological competence. Overall, we identified a total of 303 unique food items eaten by 13 immatures during ~4700 observation hours over 8.5 years of individual's development prior to independence (Fig. 1c, Supplementary Fig. 2,3). Note that diet profiles could be assessed over more observation hours than peering and exploration rates, because only a subset of observers recorded all occurrences of the latter two behaviours. For eight of the 21 immatures that were used to quantify peering and exploration rates, we had too few observation hours to reliably calculate the age-dependent increase in the breadth of their diet profiles (see Methods). Therefore, these eight immatures were not included in our subsequent analyses. By restricting our dataset to successful feeding events, rather than also including attempted feeding events, we investigated not only whether immatures learn what to eat but also how to process food to permit ingestion[34].

Individual variation in learning propensities predict substantial differences in ecological competence at independence

We modelled the breadths of the dietary profiles that immatures achieved at independence as a function of their estimated average peering and IIE rates extracted from M1. Diet profiles broaden rapidly during early development and then plateau towards the end of the dependency period (Supplementary Fig. 3). We modelled this nonlinear effect of age through the Michaelis-Menten (MM) equation, implemented using a Bayesian framework. The breadth of the dietary profile at independence is represented by the V_{max} parameter of the MM equation, henceforth the parameter is called the breadth of the dietary profile. Based on our hypothesis, we modelled the breadth of the dietary profile as a function of the interaction between estimated average peering and IIE rates (NM1).

The interaction between estimated average peering and IIE rates significantly predicted the breadth of the dietary profile (Supplementary Table 3, Fig. 4a, where the effect size of the interaction effect is represented by the difference in the effect of peering on diet breadth across the three IIE levels). Specifically, we found a significant negative effect of the interaction on the breadth of the dietary profile at independence (Estimate [95%CI] = -36.65 [-70.11, -3.82] food items).

With increasing social and asocial information-seeking propensities, immatures develop a broader ecological competence

Immatures with the highest peering and IIE rates developed the broadest diet profile by the onset of independence (Fig. 4a). In addition, the effect of peering on diet profile development became more pronounced when exploration rates decreased (negative interaction effect). Among immatures with the highest rates of IIE, those who peered at the highest rates had developed diet profiles that were 1.2 times the diet profiles of immatures who peered at lower rates (Fig. 4b). Under lower rates of IIE, the diet profiles of those who peered at the highest rates were 1.5 times larger than those who peered at lower rates (Fig. 4b).

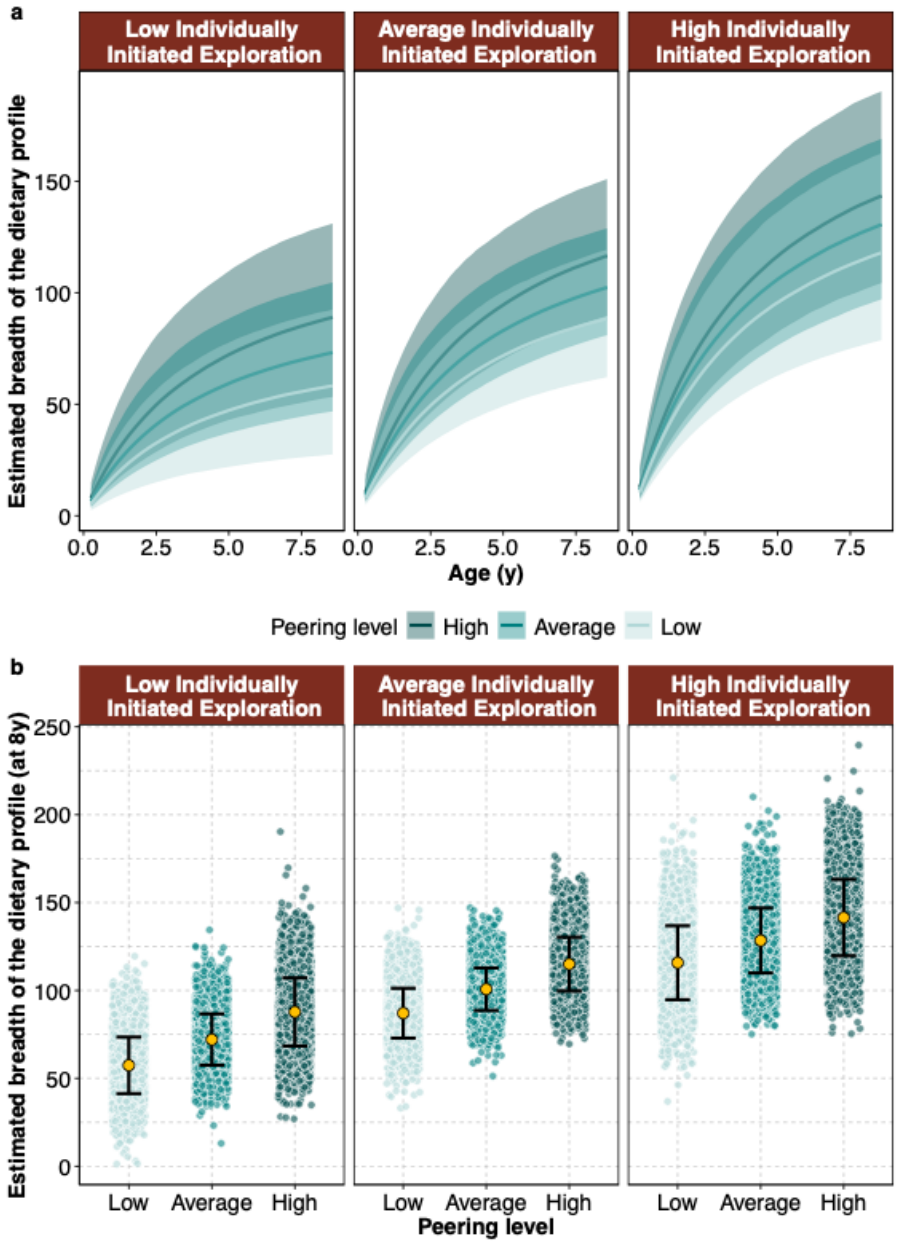


Fig. 4. Effect of social and asocial information-seeking propensities on the development of ecological competence. a. Diet profile development of immatures between birth and onset of independence (model predictions from NN1 fit with Michaelis-Menten curves; breadth of the dietary profile was modelled as function of a nonlinear interaction term; see Methods). b. Estimated breadth of the dietary profile at independence as a function of individuals' average estimated peering and individually initiated exploration rates. Low, Average, High refer to mean-1SD, mean, and mean+1SD. Each circle represents a posterior prediction. The yellow circle represents the posterior mean, and the vertical lines represent 95% CI.

To investigate the contribution of peering without follow up exploration to diet profile development, we first quantified peering events that were not followed by SIE. We found that only one-fourth (*N*=529) of all peering events were not followed by an SIE event. Furthermore, in only 15% of the follow days (*N*=39 days), a peering event occurred without any exploration event, showing that information seeking through peering alone is rare (Supplementary Fig. 6). We also found that most of the peering events without a following SIE occurred towards the end of the dependency period (Supplementary Fig. 6). Finally, in our data set we did not have any immatures that consistently peered without subsequent SIE (Supplementary Fig. 6). The rarity of peering events not followed by SIE prevented us from modelling the separate contributions of such peering and SIE to ecological competence development.

Discussion

Ours is the first study of a wild nonhuman animal on the scale necessary to assess how episodes of both social and asocial learning across the whole period of pre-independence shape the acquisition of a broad ecological competence. In orangutans, this spans an unusually long period in excess of eight years, at the end of which immatures begin to range independently of their mother. The expansive scale of our study yielded a series of discoveries that represent substantial new advances in the science of cultural evolution. First, we found that once we controlled for the potential confounding effects of age, sex, number of association partners, food availability and observation time, the remaining variation in what we called *individual* propensities for peering and exploration was nevertheless large. The relative expression of these different, major forms of learning thus appears to vary substantially between individuals, as has been shown to be the case in human children[28]. Consistent individual biases in reliance on social learning have similarly been shown across repeated experimental tests in captive apes[29] and wild chimpanzees[14]. While studies on other taxa provide mixed evidence for covariation between individuals' experimentally measured social and asocial learning abilities[30–32], we found that individuals' natural reliance on peering, IIE and SIE did not covary. The absence of a negative correlation between individuals' reliance on social and asocial learning argues against trade-offs between investment in the two forms of learning and thus against strict behavioural specialization in the wild[44].

The substantial individual variation we documented highlights the importance of investigating learning as more than a species-typical trait. This should be remembered whenever a study aims to compare different species' tendencies for cultural or asocial learning based only on averages. Individual variation in learning can emerge over evolutionary time if the benefits of learning are unpredictable, as suggested by a recent simulation study[45]. We found that individual variation was lower in rates of peering than in IIE, suggesting there may a selection pressure on maintaining rates of peering, but not IIE, above a significant threshold. This may be because IIE likely carries significant risks in the wild[21]. We also found that individual variation was higher in rates of SIE than peering, which could stem from systematic differences in the complexity of the food items to which individual immatures are exposed. Previous research has found close similarities between mother-offspring diet profiles in wild orangutans, while mothers themselves differed in their diet compositions[46,47]. Because orangutan diets vary in processing complexity, mothers may differ also in the overall complexity of their diet profiles. As less complex foods require less exploration after peering[16], immatures of such mothers might engage in lower levels of socially induced exploration (SIE), potentially contributing to greater variation in SIE than in peering. The level of individual variation in social and asocial learning propensities observed in this study is surprising, as learning propensities are likely tied to fitness and, therefore may have important consequences in many species, including in non-WEIRD humans. Therefore, individual differences in learning merit further investigation, especially through longitudinal field studies, to understand their underlying causes, which may be environmental, developmental, and/or genetic[48].

A second major finding was that, in general, peering exerts an influence on exploration for as long as around two-and-a-half hours. This leads us to suggest a distinction between what we label here as "Socially Initiated Learning" (SIL) stimulated by peering within this period— which we accordingly place within the broader conception of social learning (Fig. 5)— and "Individually Initiated Learning" (IIL) that occurs at other times. This important distinction should now be taken into account when refining the "Experience-Weighted Attraction" models that are beginning to proliferate. Hitherto they have typically made only a simple binary distinction between events labelled as social versus asocial[6,24–27], whereas we find that the greatest proportion of exploration, in the form of SIL, is consequent on peering and thus falls at the intersection between social and asocial learning. Correlations between social and asocial learning at the individual or population level must be thus interpreted with caution to avoid false positives. SIL occurs at a rate six times higher than IIL and likely involves selective exploration of the peered-at-food-item[15]. It is easy to appreciate that learning through peering alone, what we call Strictly Social Learning (SSL), and SIL may act synergistically in diet profile development. Peering stimulates SIL, and through effects such as prompting individuals to practice recently observed activities, allows maturing individuals to gradually perfect their skills, including complex skills such as tool use[49]. Indeed, our study demonstrates that during most of the developmental period, immatures engage in both SSL and SIL, which poses a challenge in estimating their individual effects. However, that these

two forms of learning often co-occur already provides evidence that both are important for the development of ecological competence in Sumatran orangutans.

Our third, overarching finding is that variation in the totality of immatures' social and asocial learning shapes the ecological competence that is so critical for achievement of independence. We believe this constitutes the most important contribution to the field of cultural evolution. Specifically, ecological competence, indexed by the breadth of the dietary profile, is predicted by an interaction between observational social learning through peering (which includes SIL and SSL) and IIL. At all levels of IIL, increases in social learning through peering led to greater ecological competence but the effect of peering on ecological competence became more pronounced as IIL decreased. This suggests that social learning through peering and IIL work synergistically in the development of diet profile (Fig. 5). Moreover, when immatures do not engage in heightened individual learning to acquire a competence, social learning through peering may compensate for the lack of individual effort.

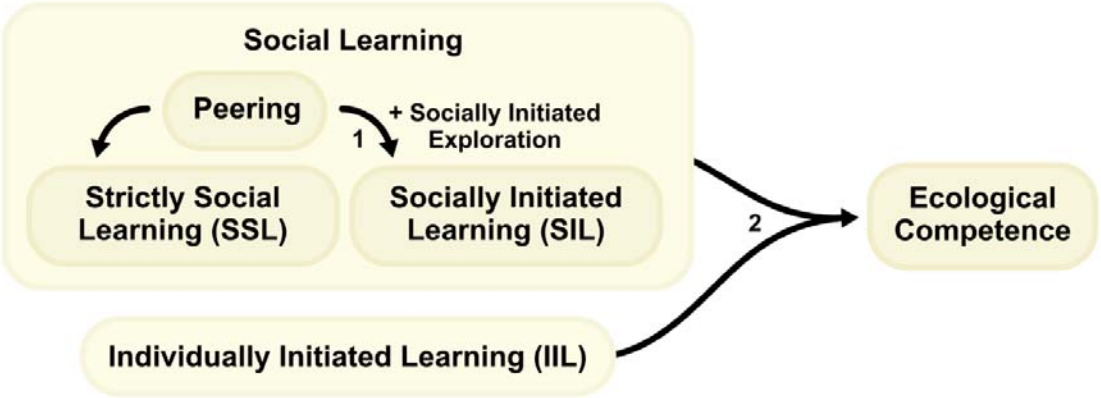


Fig. 5. Overview of the forms of learning involved in diet profile development in Sumatran orangutans. 1. Peering triggers socially initiated learning and 2. Social learning and individually initiated learning synergistically influence ecological competence development.

In contrast to SSL and SIL, cases of IIL are distinguished by their lack of direct behavioural linkage to peering, but we suggest two potential answers for how and why IIL interacts with peering to enhance ecological competence. At the developmental level, increased engagement in social learning expands an individual's pool of affordances, thereby enhancing their overall learning ability, as predicted by the Cultural Intelligence Hypothesis[50,51]. In our study, immatures with increased social learning through peering and IIL rates developed the broadest diet profile. However, we did not find a positive correlation of peering and IIL within individuals, which would be expected if these developmental effects were driving the interaction between IIL and peering. Part of the answer may be that memory of earlier peering still shapes their content well beyond the empirically derived cutoff, which may be why we find a positive correlation between peering and total exploration (sum of SIE and IIE). Furthermore, the temporal gap may facilitate adaptive exploration of behavioural

variations at the fringes of what had been learned through peering. Truskanov and Prat recently suggested that in an uncertain world, copying observed actions imperfectly, coupled with a degree of trial-and-error learning, may be the most adaptive strategy[22]. Their simulations support this idea and highlight trial-and-error learning as a stabilizing force in cultural transmission. This is likely relevant to our orangutan population and indeed to many other species.

The cultures of the great apes have been shown to be the most complex among nonhuman animals in the extensive arrays of traditions that differ between communities[52-54]. Research on chimpanzees led these studies in the later part of the twentieth century[55] but the more recent recognition and validation of peering as an index of social learning in orangutans[15], much reinforced by the present study, indicates that culture pervades apes' lives to a greater extent than the earlier studies had indicated, with individuals of the Suaq population learning socially in as many as 195 different contexts[35]. The present study extends such understanding of the pervasiveness of cultural learning in great apes into another dimension, documenting episodes of peering across eight years of immatures' development and establishing their impact on achieving the extensive and crucial dietary breadth that sustains their mature, independent foraging. Other, more focused studies have shown that cultural learning additionally pervades apes' later lives too, as when maturing males selectively peer at adult males, the optimal models for their larger-bodied mature foraging needs[36], and at resident ("expert") individuals when they migrate into new ranges[37]. Importantly, the study also highlights that cultural learning acts in synergy with asocial learning.

Our overall findings can thus be summarised as demonstrating a greater depth and pervasiveness of culture in a great apes' lives than previously demonstrated, but also a more nuanced reality in terms of the linkages between the social and asocial components of learning. All of these bring great ape culture closer to the complexities of human culture. Since orangutans, the other great apes and humans share a common ancestry, it is apparent that the extraordinary heights of human culture were likely built on already substantial evolutionary foundations.

Acknowledgements We thank all the dedicated field staff, students, and research assistants – in particular, Anais van Cauwenberghe, Ellen Meulman, Lara Nellissen, Natalie Oliver Caldwel, Sofia Forss, – who, besides CS, collected most of the data used in this study. We are grateful to the Indonesian State Ministry for Research and Technology (BRIN-RISTEK), the Directorate General of Natural Resources and Ecosystem Conservation–Ministry of Environment and Forestry of Indonesia (KSDAEKLHK), the Ministry of Internal Affairs, Indonesia, the Sumatran orangutan conservation Program (SOCP), Balai Besar Taman Nasional Gunung Leuser (TNGL), in particular Arif Saifudin, Zakir, and Samsul Amar, and all staffs in Medan for their permission and support to conduct this study. We thank Universitas Nasional (UNAS) for their support and collaboration. We thank Elliot Howard-Spink for useful discussions about the analysis. We thank Tri Rahmaeti for coordinating our

research permits and liaising with Indonesian offices and institutions. We thank the technical assistants, Richard Young and Francois Lamarque, for maintaining the SUAQ database.

Funding This work was funded by the Marie Sklodowska-Curie Actions postdoctoral fellowship (T.R.), Max Planck Institute of Animal Behavior (C.S.), the University of Zurich (C.S.), the A.H. Schultz Foundation (C.S.), the Leakey Foundation (Primate Research Fund and project grant) (C.S.), the SUAQ Foundation (C.S.), the Volkswagen Stiftung (Freigeist fellowship to C.S.), the Stiftung für Mensch und Tier (Freiburg i.Br. to C.S.).

Author contributions T.R.: conceptualization, data curation, funding acquisition, formal analysis, methodology, validation, visualization, writing—original draft, writing—review and editing. M.T.W: data curation, writing—review and editing. S.S.U-A: research administration, writing—review and editing. T.M.S.: research administration, writing—review and editing. I.R.: visualization, writing—review and editing. C.P.v.S.: writing—review and editing. A.W.: context setting, writing—original draft, writing—review and editing. P.B.: methodology, validation, supervision, writing—review and editing. C.S.: conceptualization, data collection, funding acquisition, investigation, methodology, research administration, supervision, writing—original draft, writing—review and editing.

Competing interests The authors declare that they have no competing interests.

References

1. Boyd, R., Richerson, P.J. & Henrich, J. The cultural niche: Why social learning is essential for human adaptation. *Proc. Natl. Acad. Sci.***108**, 10918-10925 (2011).

2. Tomasello, M. The ontogeny of cultural learning. *Curr. Opin. Psychol*. **8**, 1-4 (2016).

3. Allen, J.A. Community through culture: From insects to whales. *BioEEJ*. **41**, 1900060 (2019).

4. Whiten, A. The burgeoning reach of animal culture. *Science*. **372**, eabe6514 (2021).

5. van Leeuwen, E.J.C., DeTroy, S.E., Haun, D.B.M. & Call, J. Chimpanzees use social information to acquire a skill they fail to innovate. *Nat. Hum. Behav*. **8**, 891-902 (2024).

6. Canteloup, C., Cera, M.B., Barrett, B.J. & van de Waal, E. Processing of novel food reveals payoff and rank-biased social learning in a wild primate. *Sci. Rep*. **11**, 9550 (2021).

7. Langlitz, N. *Chimpanzee Culture Wars: Rethinking Human Nature alongside Japanese, European, and American Cultural Primatologists*. (Princeton University Press, 2020).

8. Boyd, R. & Richerson PJ. *The Origin and Evolution of Cultures*. (Oxford University Press, 2005).

9. Brakes, P., Aplin, L., Carroll, E.L., Greggor, A.L., Whiten, A. & Garland, E.C. Animal culture: conservation in a changing world. *Phil. Trans. R. Soc. B*. **380**, 20240127 (2025).

10. Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W. & Gruber, T. Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLOS Biol*. **12**, e1001960 (2014).

11. Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cockburn, A., Thornton, A. & Sheldon, B.C. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*. **518**, 538-541 (2015).

12. Perry, S. Conformism in the food processing techniques of white-faced capuchin monkeys (Cebus capucinus). *Anim. Cogn*. **2**, 705-716 (2009).

13. Lonsdorf, E.V., Eberly, L.E. & Pusey, A.E. Sex differences in learning in chimpanzees. *Nature*. **428**, 715-716 (2004).

14. Berdugo, S., Cohen, E., Davis, A.J., Matsuzawa, T. & Carvalho, S. The ontogeny of chimpanzee technological efficiency. *bioRxiv*. (2024).

15. Schuppli, C., Meulman, E.J.M., Forss, S.I.F., Aprilinayati, F., van Noordwijk, M.A., van Schaik, C.P. Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Anim. Behav*. **119**, 87-98 (2016).

16. Howard-Spink, E., Tennie, C., Setia, T.M., Perawati, D., van Schaik, C.P., Barrett, B., Whiten, A. & Schuppli, C. Culture is critical in driving orangutan diet development past individual potentials. *bioRxiv*. (2025).

17. Whiten, A., Horner, V. & de Waal F.B.M. Conformity to cultural norms of tool use in chimpanzees. *Nature*. **437**, 737-740 (2005).

18. Bridges, A.D., Royka, A. & Wilson, T. Lockwood, C., Richter, J., Juusola, M. & Chittka, L. Bumblebees socially learn behaviour too complex to innovate alone. *Nature*. **627**, 572-578 (2024).

19. Whiten, A. & van de Waal E. The pervasive role of social learning in primate lifetime development. *Behav. Ecol. Sociobiol*. **72**, 80 (2018).

20. Whitehead, H. & Rendell, L. *The Cultural Lives of Whales and Dolphins*. (University of Chicago Press, 2014).

21. Forss, S.I.F., Koski, S.E. & van Schaik, C.P. Explaining the paradox of neophobic explorers: The social information hypothesis. *Int. J. Primatol*. **38**, 799-822 (2017).

22. Truskanov, N. & Prat, Y. Cultural transmission in an ever-changing world: trial-and-error copying may be more robust than precise imitation. *Phil. Trans. R. Soc. B*. **373**, 20170050 (2018).

23. van Schaik, C.P. & Pradhan, G.R. A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. *J. Hum. Evol*. **44**, 645-664 (2003).

24. Hoppitt, W., Samson, J., Laland, K.N. & Thornton, A. Identification of learning mechanisms in a wild meerkat population. *PLOS ONE*. **7**, e42044 (2012).

25. Kendal, R., Hopper, L.M., Whiten, A., Brosnan, S.F., Lambeth, S.P., Schapiro, S.J. & Hoppitt, W. Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evol. Hum. Behav*. **36**, 65-72 (2015).

26. Barrett, B.J., McElreath, R.L. & Perry, S.E. Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. *Proc. R. Soc. B.* **284**, 20170358 (2017).

27. Aplin, L.M., Sheldon, B.C. & McElreath, R. Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. *Proc. Nat. Acad. Sci*. **114**, 7830-7837 (2017).

28. Flynn, E., Turner, C. & Giraldeau, L.A. Selectivity in social and asocial learning: investigating the prevalence, effect and development of young children's learning preferences. *Phil. Trans. R. Soc. B.* **371**, 20150189 (2016).

29. Watson, S.K., Vale, G.L., Hopper, L.M., Dean, L.G., Kendal, R.L., Price, E.E., Wood, L.A., Davis, S.J., Schapiro, S.J., Lambeth, S.P. & Whiten, A. Chimpanzees demonstrate individual differences in social information use. *Anim. Cogn*. **21**, 639-650 (2018).

30. Bouchard, J., Goodyer, W. & Lefebvre, L. Social learning and innovation are positively correlated in pigeons (Columba livia). *Anim. Cogn*. **10**, 259-266 (2007).

31. Burkart, J.M., Strasser, A. & Foglia, M. Trade-offs between social learning and individual innovativeness in common marmosets, Callithrix jacchus. *Anim. Behav*. **77**, 1291-1301 (2009).

32. Toyokawa, W., Saito, Y. & Kameda, T. Individual differences in learning behaviours in humans: Asocial exploration tendency does not predict reliance on social learning. *Evol. Hum. Behav*. **38**, 325-333 (2017).

33. van Schaik, C.P. & Burkart, J.M. Social learning and evolution: the cultural intelligence hypothesis. *Phil. Trans. R. Soc. B.* **366**, 1008-1016 (2011).

34. Schuppli, C., Forss, S.I.F., Meulman, E.J.M. Zweifel, N., Lee, K.C., Rukmana, E. Vogel, E.R., van Noordwijk, M.A. & van Schaik, C.P. Development of foraging skills in two orangutan populations: needing to learn or needing to grow? *Front. Zool*. **13**, 43 (2016).

35. Schuppli, C. & van Schaik, C.P. Animal cultures: how we've only seen the tip of the iceberg. *Evol. Hum. Sci*. **1**, e2 (2019).

36. Ehmann, B., van Schaik CP, Ashbury AM, Mörchen, J., Musdarlia, H., Utami-Atmoko, S.S., van Noordwijk, M.A. & Schuppli, C. Immature wild orangutans acquire relevant ecological knowledge through sex-specific attentional biases during social learning. *PLoS Biol*.**19**, e3001173 (2021).

37. Mörchen, J., Luhn, F., Wassmer O, Kunz, J.A., Kulik, L., van Noordwijk, M.A., van Schaik, C.P., Rianti, P., Utami-Atmoko, S.S., Widdig, A. & Schuppli, C. Migrant orangutan males use social learning to adapt to new habitat after dispersal. *Front. Ecol. Evol*. **11**, 1158887 (2023).

38. Heyes, C. What's social about social learning? *J. Comp. Psychol*. **126**, 193-202 (2012).

39. Schuppli, C., Cauwenberghe, A.V., Setia, T.M. & Haun, D. The ontogeny of exploratory object manipulation behaviour in wild orangutans. *Evol. Hum. Sci*. **3**, e39 (2021).

40. Laumer, I.B., Kansal, S., van Cauwenberghe, A., Rahmaeti, T., Setia, T.M., Mundry, R., Haun, D. & Schuppli, C. Wild and zoo-housed orangutans differ in how they explore objects. *Sci. Rep*. **15**, 14853 (2025).

41. Schuppli, C., Forss, S., Meulman, E., Utami-Atmoko, S.S., van Noordwijk, M.A. & van Schaik, C.P. The effects of sociability on exploratory tendency and innovation repertoires in wild Sumatran and Bornean orangutans. *Sci. Rep*. **7**, 15464 (2017).

42. Mörchen, J., Luhn, F., Wassmer, O., Kunz, J.A., Kulik, L., van Noordwijk, M.A., Rianti, P., Rahmaeti, T., Utami-Atmoko, S.S.U., Widdig, A. & Schuppli, C. Orangutan males make increased use of social learning opportunities, when resource availability is high. *iScience*. **27** (2024).

43. Singleton, I. & van Schaik, C.P. Orangutan home range size and its determinants in a Sumatran swamp forest. *Int. J. Primatol*. **22**, 877-911 (2001).

44. Laland, K.N. Social learning strategies. *Learn. Behav*. **32**, 4-14 (2004).

45. van den Berg, P., Vu, T. & Molleman, L. Unpredictable benefits of social information can lead to the evolution of individual differences in social learning. *Nat. Commun.* **15**, 5138 (2024).

46. Jaeggi, A.V., Dunkel, L.P., van Noordwijk, M.A., Wich, S.A., Sura, A.A.L. & van Schaik, C.P. Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *Am. J. Primatol*. **72**, 62-71 (2010).

47. Schuppli, C., Utami-Atmoko, S.S., Vogel, E.R., van Schaik, C.P. & van Noordwijk, M.A. The development and maintenance of sex differences in dietary breadth and complexity in Bornean orangutans. *Behav. Ecol. Sociobiol*. **75**, 81 (2021).

48. Mesoudi, A., Chang, L., Dall, S.R.X. & Thornton, A. The evolution of individual and cultural variation in social learning. *TREE*. **31**, 215-225 (2016).

49. Whiten, A. Experimental studies illuminate the cultural transmission of percussive technologies in Homo and Pan. *Phil. Trans. R. Soc. B.* **370**, 20140359 (2015).

50. van Schaik, C.P. & Burkart, J.M. Social learning and evolution: the cultural intelligence hypothesis. *Phil. Trans. R. Soc. B.* **366**, 1008-1016 (2011).

51. Whiten, A. & van Schaik, C.P. The evolution of animal ‘cultures’ and social intelligence. *Phil. Trans. R. Soc. B.* **362**, 603-620 (2007).

52. Robbins, M.M., Ando, C., Fawcett, K.A., Grueter, C.A., Hedwig, D., Iwata, Y., Lodwick, J.L., Masi, S., Salmi, R., Stoinski, T.S., Todd, A., Vercellio, V. & Yamagiwa, J. Behavioral variation in gorillas: evidence of potential cultural traits. *PLOS ONE.* **11**, e0160483 (2016).

53. Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.EG., Wrangham, R.W. & Boesch, C. Charting cultural variation in chimpanzees. *Behaviour*. **138**, 1481-1516 (2001).

54. van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., Suzuki, A., Utami-Atmoko, S.S. & Merrill, M. Orangutan cultures and the evolution of material vulture. *Science*. **299**, 102-105 (2003).

55. Whiten, A. The second inheritance system of chimpanzees and humans. *Nature*. **437**, 52-55 (2005).

Methods

Data Collection

This research was approved by the Indonesian State Ministry for Research, Technology and Higher Education, the National Research and Innovation Agency (BRIN RISTEK; Research Permit No.: 152/SIP/FRP/SM/V/2012), the Directorate General of Natural Resources and Ecosystem Conservation under the Ministry of Environment and Forestry of Indonesia (KSDAE-KLHK) and the Gunung Leuser National Park (TNGL). This research was conducted in accordance with the Indonesian law and the ethical standards for research on non-human primates, following the Guidelines for the Treatment of Animals in Behavioural Research and Teaching of the Association for the Study of Animal Behaviour[54].

We investigated whether immatures I. engage more frequently in social or asocial learning, II. show distinct individual propensities for both social and asocial learning and these propensities are correlated at the individual level, and III. their levels of social and asocial learning affect their development of ecological competence, and the effect of one learning mode depends on the level of engagement in the other in Sumatran orangutans (*Pongo abelii*). To address these questions, we used longitudinal and cross-sectional data collected from 2007 to 2019 at the Suaq Balimbing research area in the Gunung Leuser National Park (3°42 N, 97°26 E) in South Aceh, Indonesia.

CS and a total of 15 other observers collected data on daily behaviour through instantaneous scan sampling at 2-minute intervals during focal animal follows following a standardized protocol (www.ab.mpg.de/571325/standarddatacollectionrules_suaq_detailed_jan204.pdf) for orangutan data collection. To quantify social and individual information seeking, we included *all occurrence* data on peering and exploration. Focal individuals were followed from the morning nest (~06:00) to the night nest (~18:00) when possible. When a focal individual could not be followed nest to nest, the follow type fell into any of the three following categories: found-to-nest, found-to-lost or nest-to-lost. All the researchers underwent a training period, and the data collected by a new researcher was included in the database only when the inter-observer reliability reached a minimum of 85% with experienced researchers for simultaneous focal follows. Nonetheless, we controlled for potential observer-to-observer differences in our models (see statistical analysis). Data collectors were blind to the aims and objectives of the current study.

We used peering behaviour to quantify socially information seeking. We defined peering as attentive and sustained (≥5 seconds) close-range (2-5 m) observation of conspecifics' behaviour[15]. From previous research on the study population, we know that peering occurs most frequently in learning-intense contexts, such as feeding and nesting[15,55]. We recorded a total of 2113 peering events by 21 focal immatures (*N*=4 females) between 0.51 and 8.72 years of age (Fig. S1) during 1759.98 *h* of observation (*N*=260 follows).

We used exploration behaviour to quantify asocial information seeking. We defined explorations as sustained, repetitive, manipulation of objects or attempted feeding – but without successful ingestion of food items[15]. Object explorations were often destructive in nature. We recorded a total of 6125 exploration events by 21 focal immatures between 0.51 and 8.72 years of age (Fig. S1) during 1743.2 *h* of observation (*N*=257 follows).

Adult Sumatran orangutan at Suaq have large diet profiles, including ~250 unique food items[16]. At each feeding activity *scan*, we noted down the species and the parts eaten by the focal individual. Following previous research, we divided parts of the species eaten into broad categories of fruits, leaves, bark, pith, and insects[30]. We considered each ingested species-part combination as one unique food item[30]. We identified a total of 303 recorded, unique food items eaten by 13 focal immatures between 0.26 and 8.57 years of age (Fig. S1) during 4792.43 *h* of observation (*N*=453 follows). We only considered feeding scans during which the immatures properly ingested the food items without the help of their mothers. We recorded a total of 51,055 feeding scans, out of which the food item was identified in 50,542 scans resulting in 1% of the feeding scans with unidentified food items (across 453 follows; Fig. S2). Note that diet profiles could be assessed over more observation hours than peering and exploration rates, because only a subset of observers recorded all occurrences of the latter two behaviours.

Each of these 13 immatures was observed in at least 2 different age years, and each focal follow was at least 5 *h* long. Beyond 5 hours, an increase in follow hours did not result in an increase in the recorded number of unique food items eaten by a focal immature. Using all the feeding scans with identified a food item, we calculated the breadth of the dietary profile as the cumulative number of unique food items eaten by each immature at each sampled age (Fig. S3), which was our measure of ecological competence. Food species were identified with the help of long-term local field assistants, all of whom had multi-year experience in identifying the species at the research site. For eight of the 21 immatures that were used to quantify peering and exploration rates, we had too few observation hours to reliably calculate the age-dependent increase in the breadth of their diet profiles. Therefore, these eight immatures were not included in our final nonlinear model to assess ecological competence.

Within the home ranges of frequently observed focal individuals, we monitored all the trees with a DBH of >10 cm along two long-term phenology transects (North-South and East-West) for the presence of unripe, semi-ripe, and ripe fruits. Each month, we quantified the

Food Availability Index from these ~1000 trees as the percentage of fruiting trees in these phenology plots[56].

We calculated daily average association size for each follow by taking the average of the number of association partners (defined as individuals within 50 m of the focal individual) across all the scans taken during a follow.

Statistical analysis

All the statistical analyses and plotting were performed using R, version 4.3.1[57]. All the graphs were generated using the *ggplot2* package[58] (version 3.5.2) or *ggraph* package[59] (version 2.2.1). This study was purely observational in nature and, therefore, did not require blinding. 95% credible intervals of the Generalized Linear Mixed Effects Models (GLMM) estimates not overlapping zero was considered to indicate a statistically significance.

When does an exploration event become independent of a peering event?

From previous research on the study population, we know that peering triggers increased selective exploration in immatures[15,54]. To determine the time point after which exploration rates return to baseline following a peering event, we first calculated the time to each exploration event following a peering event and before the next peering event. We then estimated the hazard function of exploration events over time since the last peering event. To do so, we used the *muhaz* package[60] (version 1.2.6.4) in R, which implements kernel-smoothed hazard estimation for time-to-event data.

To identify the point at which the hazard (i.e., the instantaneous rate of exploration) stabilized—implying independence of exploration events from the preceding peering event—we computed the first derivative of the hazard function (i.e., its slope) across time. A sustained near-zero slope indicates a flattening of the hazard curve, meaning that after this point in time the probability of exploration is no longer dependent on the last peering event. To avoid spurious identifications due to short-term fluctuations in exploration rate, we checked whether the near-zero slope remained stable for at least 25 continuous timepoints. We implemented this condition using a moving window approach using the *zoo* package[61] (version 1.8-14). Based on the estimated time points (see Results), we split the exploration events into two: socially initiated exploration events (SIE, ≤145 minutes since the preceding peering event and till the next peering event) and individually initiated exploration events (IIE, >145 minutes since the preceding peering event and till the next peering event).

Since not all follows began from immatures' morning nests, we could not include the exploration events that occurred before any peering event in a day in the calculations for exploration events that were independent of peering. However, 77% of the follows used for the analysis were nest-to-nest follows. In addition, since not all follows ended at immatures' night nests, to avoid any systematic variation across the follows or immatures, we calculated the number of exploration events that were independent of peering using only the exploration

events that occurred between two peering events, regardless of the follow type (*N*=4649 exploration events). This did not affect our sample size (i.e., focal follow days).

The models were fit using a Bayesian approach using *Stan*, version 2.32.2[62,63] through the *brms* package, version 2.22.0[64]. All the models were run for 4 chains with 2000 iterations each, out of which 1000 were warm-up iterations, leading to 4000 samples for each model estimate. To prevent divergent transitions, we set adapt_delta to 0.99, step size to 0.01 and maximum tree depth to 15. We used the 'bayes_R2' function of the *brms* package to calculate R^2 to assess model fit[65].

I & II <u>Do immatures engage more frequently in social or asocial learning and show distinct individual social and asocial learning propensities that are correlated at the individual level?</u>
We fit four univariate Generalized Linear Mixed Effects Models (GLMM), for peering (U1), SIE (U2), IIE (U3), and total exploration (U4), with all the predictors and random intercepts and slopes (see below). The number of recorded information-seeking events during each follow was the dependent variable in each of the models. We refer to these as full models. We then fit reduced models, which lacked the random effects of immature ID but contained all other predictors and random effects. We refer to these as reduced models. We compared the full and the reduced model using leave-one-out cross-validation[66] through the *loo* function of the *brms* package and considered individual variation to be substantial if the full model had the highest ELPD value – i.e., the highest predictive value.

Since there was significant variation among immatures in all four information-seeking rates (see Results), to determine whether peering and exploration rates were correlated at the immature-level, we fit a multivariate GLMM. Here again we used the number of recorded information-seeking events during each follow as the dependent variable.

We used *brms*' default (uninformative) priors for the univariate and multivariate models. We fit the models using a negative binomial error distribution and a log link function.

Predictors: Since the observation duration varied across the follows, we used it as an offset, supplied through the 'rate' function of the *brms* package. We included age and sex (male/female) of the focal individual, FAI, and daily average association size during a follow as predictors of information-seeking rates to control for their influence on these variables[15,30,32,37,38]. Since peering peaks around 3-4 years of age in the study population[15], we additionally included a quadratic effect of age in the peering model. As there were slight differences in the number of follows used for peering *vs* exploration (N=260 *vs* 257), we used the 'subset' function of the *brms* package to choose the appropriate follows for analyzing each behaviour. For easier interpretation of model estimates and to ease model convergence, we *z*-standardized the continuous predictors (age, daily average association size, and FAI) to a mean of 0 and a standard deviation of 1 and dummy coded and centered the categorical predictor.

Random effects: We used maximal random effects structure in all the multivariate models. We included immature identity as a random intercept, as we were interested in the random intercept estimates, and age, daily average association size and FAI as random slopes within immature identity. The random intercepts from the peering model represent the *estimated average peering rates* and those from the exploration models represent the *estimated average SIE, IIE, and total exploration rates* for each focal immature during development. As we included *all occurrence* data, we included observer as an additional random intercept to control for observer-to-observer differences in sampling.

The multivariate model then allowed us to test whether there was a correlation between different *estimated average rates* while accounting for the error associated with these estimates. To this end, we did a directional hypothesis test to check whether the correlation estimate (N=4000 samples) was different from 0 (r>0) using the 'hypothesis' function of the *brms* package.

We fit four multivariate models based on datasets including: M1. peering and IIE events, M2. peering and SIE events, M3. SIE and IIE events, and M4. peering and total exploration events. Furthermore, we used the estimates from M1, based on the 145-minute cut-off dataset, to do the subsequent nonlinear analysis (outlined under III).

We assessed model convergence through R-hat values[67], which were equal to 1.00, and bulk and tail ESS, which were all >1000. We also visually inspected the trace plots and found no model convergence issues.

III <u>Do the levels of social and asocial learning affect the development of ecological competence and whether the effect of one learning mode depends on the level of engagement in the other?</u>

To investigate the development of ecological competence, we analyzed the breadth of the diet profile. We modelled it as a nonlinear function of age using the Michaelis-Menten (MM) equation[68]. This is because from previous research we know that the breadth of the diet profile increases with age but approaches an upper asymptote towards independence[30]. MM equation is used in enzymatic kinetics and describes the transformation of a substrate into a product with the help of two parameters, $V_{\max}$ and K [1].

$$\text{Breadth of dietary profile} \sim Base + \frac{V_{max} * Age}{K + Age} \qquad [1]$$

In the context of diet profile, $V_{\max}$ represents the maximum breadth of the diet profile or the cumulative number of unique food items that an immature has eaten by the onset of independence (~8.5 years in the current dataset). This is the upper asymptote of the MM curve. K represents the half-saturation age or the age at which an immature reaches 50% of $V_{\max}$. K controls how quickly the breadth of the diet profile approaches $V_{\max}$. We modelled $V_{\max}$ and K with a softplus transformation to constrain them to positive values. We modelled

V_{max} as a function of an interaction between estimated average peering rate and estimated average IIE rate during development to predict the interactive effect of social and asocial information-seeking rates on ecological competence. We scaled the estimates using the 'scale' function to ease the interpretation of model coefficients.

Since previous research found that the breadth of the diet profiles differed between male and female immatures[4], we modelled both V_{max} and K as a function of immature sex. As there were repeated samples for each immature, we included the random intercepts of immature identity in these two parameters. We refer to this model as NM1. Apart from this model with a linear interaction term, we built another nonlinear model (NN1) where we modeled V_{max} as a nonlinear function of these rates, using a smooth interaction term s(peering, individually initiated exploration, k = 5), where k specifies the number of basis functions used to approximate the smooth surface[69]. This provides a balance between model flexibility and parsimony, allowing moderate curvature while reducing the risk of overfitting. In this way, the nonlinear interactions allowed us to capture the complex, interdependent relationship between social and asocial information-seeking rates on diet acquisition, which are unlikely to interact in a strictly linear fashion. For example, the benefit of peering may depend on the level of exploration, or *vice versa*, which is impossible to be captured by a simple, linear interaction term. Since the estimates of the model with the smooth interaction term is not interpretable, we report the model estimates from NM1 but present the graph based on NN1.

We used weakly informative priors to regularize parameter estimation while allowing the data to dominate. For the baseline diet breath (base), we set a truncated normal prior of N(0,5), as immatures are dependent on their mothers for nutrition at birth. We set normal priors of N(150,10) for the intercept, as the maximum cumulative diet breadth was ~150 in our data set (Fig. S3) and previous simulation-based research found that immatures' diet breadth reaches up to ~225[16]; N(15,4) for the effect of sex, as previous research found a 10% difference in diet breadth between the sexes towards independence[43]; N(0,4) for estimated peering and IIE rates; and N(0,10) and N(0,2) for the random intercept of immature identity for V_{max} and K, respectively. We set normal priors of N(2,1) and N(1,0.5) for the intercept and the effect of sex, respectively, for the K parameter, as it can be discerned from previous research that immatures reached 50% adult-like diet breadth between 2 and 4 years with a 1-2 year difference between males and females[30,43]. We selected these priors to reflect biologically plausible ranges while minimizing undue influence on the posterior. We did not set informative priors for the interaction between peering and IIE because no prior knowledge of this effect was available. Instead, we used the default flat prior in *brms* for the interaction term to avoid imposing unwarranted assumptions on the model.

All R-hat values were equal to 1.00, and all bulk and tail ESS were >2000. Visual inspection of the trace plots showed no model convergence issues.

Data and materials availability All processed data and codes will be publicly made available via an open access data repository upon publication.

References

54. ASAB Ethical Committee/ABS Animal Care Committee. Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching. *Anim. Behav.* **207**, I-XI (2024).

55. Permana, A., Permana, J., Nellissen, L., Prayogi, E.S., Prasetyo, D., Wich, S.A., van Schaik, C.P. & Schuppli, C. Observational social learning of “know-how” and “know-what” in wild orangutans: Evidence from nest-building skill ccquisition. *Nat. Comm*. **8**, 890 (2025).

56. Vogel, E.R., Alavi, S.E., Utami-Atmoko, S.S.U., van Noordwijk, M.A., Bransford, T.D., Erb, W.M., Zulfa, A., Sulistyo, F., Farida, W.R. & Rothman, J.M. Nutritional ecology of wild Bornean orangutans (Pongo pygmaeus wurmbii) in a peat swamp habitat: Effects of age, sex, and season. *Am. J. Primatol*. **79**, e22618 (2017).

57. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (2021). See https://www.r-project.org/.

58. Wickham, H. Data analysis. In *ggplot2: elegant graphics for data analysis* 189-201 (Springer international publishing, 2016).

59. Pedersen, T. *ggraph: An Implementation of Grammar of Graphics for Graphs and Networks*. (v 2.2.1.9000) (2024). See https://ggraph.data-imaginist.com.

60. Hess, K. muhaz: Hazard function estimation in survival analysis. (2021). See https://cran.r-project.org/web/packages/muhaz/index.html

61. Zeileis, A. & Grothendieck, G. zoo: S3 Infrastructure for regular and irregular time series. *J Stat. Softw*. **14**, 1-27 (2005).

62. Stan. See https://mc-stan.org/.

63. Stan Development Team. Stan Reference Manual (v. 2.32.5). (2023). See https://mc-stan.org/docs/reference-manual/.

64. Bürkner, P.C. brms: An R Package for bayesian multilevel models using Stan. *J. Stat. Softw*. **80**, 1-28 (2017).

65. Gelman, A., Goodrich, B., Gabry, J. & Vehtari A. R-squared for bayesian regression models. *Am. Stat*. **73**, 307-309 (2019).

66. Vehtari, A., Gelman, A. & Gabry, J. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput*. **27**, 1413-1432 (2017).

67. Vehtari, A., Gelman, A., Simpson, D., Carpenter, B. & Bürkner, P.C. Rank-normalization, folding, and localization: An improved Rˆ for assessing convergence of MCMC (with Discussion). *Bayesian. Anal*. **16**, 667-718 (2021).

68. Michaelis, L. & Menten, M.M.L. Die Kinetik der Invertinwirkung. *Biochemische Zeitschrift*. **49**, 333-369 (1913).

69. Wood, S.N. Thin plate regression splines. *J. R. Stat. Soc. Ser. B. Stat. Methodol*. **65**, 95-114 (2003).