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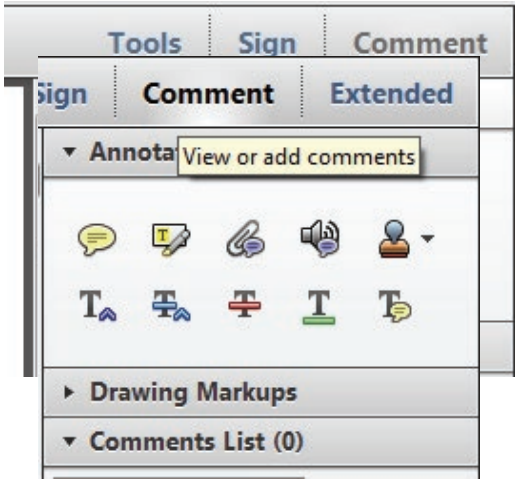

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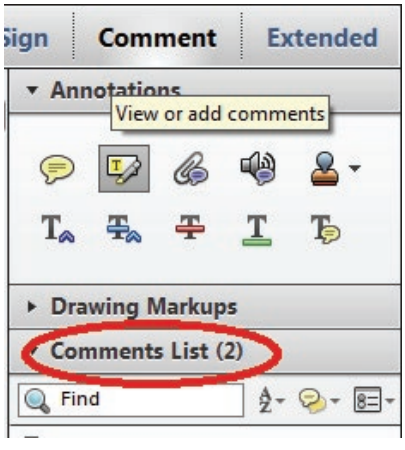

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LEARNING

How 8 years of social and individual learning interact to shape ecological competence in orangutans

Revathe Thillaikumar[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]*

Cultural learning permeates human skill and knowledge acquisition. To understand its importance for nonhuman apes, we analyzed just under 7000 records of behavioral bouts of social and individual learning across wild orangutans' 8-year dependency period to assess their combined effects on ecological competence, which is crucial for independent survival. Social learning was five times more frequent than individual learning and influenced subsequent learning for hours. Immature orangutans varied substantially in their learning propensities, and those with heightened social and individual learning propensities developed the most expansive diet profiles at independence. Furthermore, social learning had a compensatory effect on diet profile development when individual learning was low. Our findings advance the science of cultural evolution by showing how multiyear social and individual learning interact to shape great apes' broad ecological competence.

Until as recently as the middle of the past century, culture was thought to be distinctly human (*1*). Recent research has revealed that to the contrary, culture defined as "information capable of affecting individuals' behavior that they acquire from other members of their species through … forms of social transmission" (*2*) is widespread in the animal kingdom, extending to all main vertebrate taxa and even invertebrates, including insects (*3*–*5*). Although social learning establishes information as cultural, such information originates from innovations (*6*), which are usually generated through individual learning processes (*7*). Therefore, culture is dependent on both social and individual learning processes (*6*).

Although social learning has garnered much of the attention in animal culture research, the concomitant role of individual learning is poorly understood. Individual learning refers to learning through one's own efforts, such as through targeted exploration and practice or iterative problem-solving, without apparent immediate social influences. Generally, individual learning is thought to be less efficient and to entail greater risks, such as poisoning and predation, than social learning (*8*). However, because individual learning enables direct assessment of current environmental conditions, it enhances information reliability and provides more complete and up-to-date information about the payoff structure and variability of different behavioral options than what socially transmitted information alone can offer (*9*). As a result, a strict reliance on social learning alone can compromise individuals' adaptability to changing conditions (*10*) and may eventually lead to repertoire erosion because of incomplete information transmission (*11*). Furthermore, especially in the case of complex skills, precise social learning of the entire skill may often not be possible. Complex skills involve unobservable elements, such as effective usage of a tool inside concealed spaces such as a tree hole to extract food items (*11*). They also comprise multiple steps, all of which cannot be observed or learned through social learning alone without independent practice (*12*), resulting in only elements—but not the whole functional sequence—of a skill being socially learned. Therefore, individual learning is likely required to learn complex skills and, in these cases, contingent upon social learning.

Although numerous studies now point to the existence of social learning capacities and pervasive cultural transmission in animals' lives (*3*–*5*, *12*–*21*), none capture the scale of what culture in the wild is thought to entail: specifically, the capacity to learn a multitude of things in the course of individuals' development, generating a corresponding breadth of competence necessary for successful adult life. In particular, how animals draw on both social and individual learning during their multiyear development to acquire such broad, survival-relevant ecological competences has remained entirely unknown.

Focusing on the Sumatran orangutan (*Pongo abelii*), we bridged this gap by testing whether and how social and individual learning during development interact to shape the extent of ecological competence acquired by immature orangutans (immatures) at weaning. Adult Sumatran orangutan diet encompasses a challenging total of around 250 different food items, many of which require preingestive processing steps (including tool use for some items), which are selected from thousands of different options in the forest (*22*). To develop their diet profiles, individuals need to learn which food items to eat (know-what), how to process them before ingestion (know-how), and when and where to find the food items (know-when and know-where, respectively). Because immatures need to independently survive in the wild after their lengthy developmental period of about 8 years, acquiring their diets while in constant association with their mothers during development is vital. Diet profile breadth (the cumulative number of different food items eaten by the time of independence) is thus a measure of broad ecological competence, with high survival relevance.

To answer our question, we examined more than 6700 detailed all-occurrence records of visual peering (Fig. 1A) and exploration (Fig. 1B) F1
behavior, collected during more than 1700 hours of detailed direct observation of 21 immatures during a 12-year period at the Suaq Balimbing research area. We sampled immatures when they were between 0.51 and 8.72 years of age (fig. S1), resulting in a total of 257 focal follows. Peering is defined as sustained, attentive, close-range observation of the behaviors of conspecifics (*23*). The Suaq orangutans are estimated to peer around 40,000 times over the course of their lifetime (*24*). After peering, immatures often engage in targeted explorations, likely to practice what they observed (*23*, *25*). This suggests that individuals may use peering to socially acquire ecological competence, including know-what and know-how components (*23*, *25*, *26*). We therefore used peering rate (number of events/hour) as a measure of an individual's propensity to engage in social learning. Exploration is a key component of individual learning (*27*, *28*). We defined exploration as sustained—often destructive—manipulation of objects or attempted feeding without successful ingestion of food items (*28*). Through exploration, individuals can find out whether an object is a food item or a substrate of a food item, or whether it can be used as a tool to access embedded food items. We thus used exploration rate as a measure of an individual's propensity to engage in individual learning.

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Fig. 1. An immature Sumatran orangutan. The immature is (**A**) peering at its mother, who is feeding on Neesia fruit (*Neesia aquatica*), and (**B**) exploring the fruit using a stick tool.

We identified a total of 303 distinct food items eaten by 13 immatures over their developmental period (table S1 and figs. S1 to S4). These data were collected through instantaneous scan sampling at 2-min intervals during ~4700 observation hours ($n = 453$ follows) to quantify the breadth of immatures' diet profiles. We considered only feeding scans during which the immatures fully ingested the food items without any preingestive processing of the food items (*23*, *29*) by their mothers.

Focal immatures were followed from the morning nest (~06:00) until the night nest (~18:00) when possible. All of the researchers underwent a training period, and the data collected by a new researcher was included for analysis only when the interobserver reliability reached a minimum of 85% with experienced researchers for simultaneous focal follows. In addition, we controlled for potential observer-to-observer differences in our models by including a random intercept for observers. Data collectors were blind to the aims and objectives of the current study.

To predict the contributions of different forms of learning to competence development in wild individuals, we developed a three-step analytical approach (Fig. 2), in which we linked an individual's average learning propensities during development to the extent of ecological competence acquired by it at the onset of independence from its mother. Previous research indicates that peering elicits an immediate increase in exploration (*23*), which suggests that not all explorations are truly indicative of individual learning, without immediate social influences. Therefore, we first conducted a hazard analysis to estimate the time point at which the instantaneous rate of exploration stabilized after a peering event, indicating a return to baseline exploration rates. Using the time cutoff indicated by the hazard analysis, we split the recorded exploration events into either socially initiated (those that occurred at or before the time cutoff) or individually initiated (those that occurred after the time cutoff) exploration events.

As a next step, we estimated the average rates of these behaviors shown by each immature during the developmental period. To do so, we analyzed the rates at which immatures engaged in peering, socially initiated exploration, and individually initiated exploration during each follow using three univariate Bayesian generalized linear mixed-effects models (U1 to U3). We controlled for age and sex of the focal individual, prevailing habitat-wide food availability, and daily average association size because they are known to influence peering and exploration in this population (*23*–*25*, *28*, *30*, *31*). We therefore refer to the resulting measures as the immatures' social, socially initiated, and individually initiated learning propensities. By controlling for the number of association partners, we accounted for any differences in social learning opportunities experienced by the focal immatures. Because these immatures live in highly overlapping home ranges (*32*), systematic habitat-induced differences in individual learning opportunities are unlikely. We included a random intercept of immature identity to estimate social and individual learning propensities of each immature and the variation in these propensities among them.

To answer our main question, as the final step, we modeled the breadths of the diet profiles as a function of the interaction between individuals' estimated average social and individually initiated learning propensities (NM1). Diet profiles broaden rapidly during early development and then plateau toward the end of the dependency period (fig. S4). We modeled this nonlinear effect of age through the Michaelis-Menten equation, implemented by use of a Bayesian framework.

Most explorations are elicited by prior peering

We observed a total of 2113 peering and 4649 exploration events over the developmental period of 21 immatures (fig. S1). On average, immatures peered at a rate of 1.25 events/hour (SD = 1.205) and explored at a rate of 3.71 events/hour (SD = 4.112), seemingly suggesting that they have a higher propensity to engage in individual than social learning. However, we found that most exploration events are far from truly individually initiated. On average, exploration events became independent of prior peering only after 145 min (fig. S5), highlighting a previously underexplored, intimate intertwining of social and individual learning at the immediate, proximate level. We therefore refer to the exploration events that occurred at or within 145 min of the preceding peering event and before the subsequent peering event as socially initiated explorations ($n = 4235$ events) and those that occurred beyond 145 min as individually initiated explorations ($n = 414$ events). Immatures individually initiated explorations at a rate of only 0.25 events/hour, (SD = 0.801), which was one-fifth and one-sixth of the peering and socially initiated exploration rates (fig. S6), respectively, indicating that truly individual learning events are relatively rare in wild orangutans.

Social and individual learning propensities are individual specific

We found variation among immatures in peering and socially initiated and individually initiated exploration propensities (table S2), indicating that on average, immatures differed substantially from one another in how much they engaged in social and socially initiated and individually initiated learning. Immatures differed from one another to a lesser extent in social learning propensity {U1, SD [95% confidence interval (CI)] = 0.69 (0.16, 1.42)} (Fig. 3A) than in socially initiated [U2: SD (95% CI) = 1.24 (0.09, 2.80)] (Fig. 3B) or individually initiated [U3: SD (95% CI) = 1.05 (0.11, 2.56)] (Fig. 3C) learning propensity. When we performed sensitivity analyses using three new thresholds to classify explorations as independent of peering (70-min, 130-min, and 160-min cutoffs), the results on individual variation in individually initiated learning propensity remained substantial (table S2, SU1 to SU3), but with shorter time cutoffs, the variation became comparable with that observed in social learning propensity (table S3, SM1 to SM3).

Within individuals, propensities of different forms of learning are not correlated

Before testing the interaction effect of social and individual learning on diet profile development, we fit three multivariate models to test for individual-level correlations among social, socially initiated, and individually initiated learning propensities. These models showed no evidence for a correlation between immatures' different learning propensities (Fig. 3, D to F, and table S3, M1 to M3). Overall, these results suggest that immatures who showed a higher propensity for social learning did not systematically also show higher propensities for other forms of learning. However, there appears to be a putative positive association between social and socially initiated learning propensities (Fig. 3E). To avoid variance inflation, we therefore did not test the combined effects of social and socially initiated learning propensities on diet profile development. However, the learning effects associated with socially initiated explorations may be implicitly captured when testing the effects of social and individually initiated

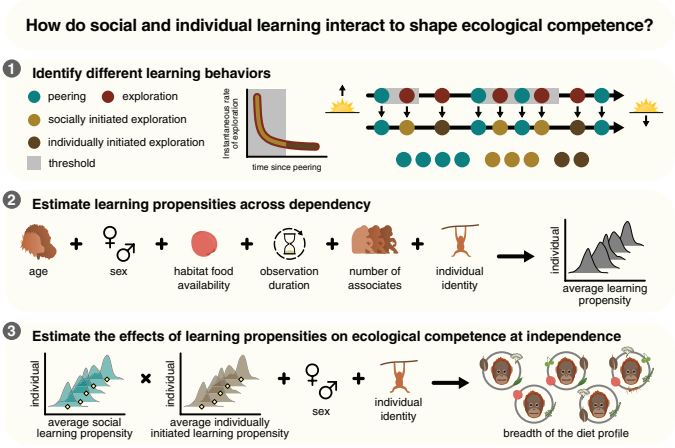

Fig. 2. Testing the effects of social and individual learning on the development of a broad ecological competence. In step 1, the first row of dots indicates immatures' peering and exploration events, which were recorded by following individuals throughout their daily active period, whenever possible. The second row illustrates how the exploration events were classified as either socially or individually initiated exploration events by using a time threshold (gray). This procedure resulted in the identification of three different forms of learning events, shown in the third row of dots. Step 2 illustrates the estimation of individuals' average learning propensities over the entire dependency period. Step 3 illustrates how we tested whether the breadths of the diet profiles at independence are predicted by individuals' learning propensities. Steps 2 and 3 are depicted as statistical models.

learning propensities on diet profile development. Last, as expected by the immediate, heightened effect of peering on explorations, a fourth multivariate model showed that total exploration, which varied substantially among immatures (table S2, U4), and peering propensities were positively correlated in immatures (table S3, M4).

With increasing social and individual learning propensities, immatures develop a broader ecological competence

The interaction between estimated average social and individually initiated learning propensities significantly predicted the breadth of the diet profile at independence (Fig. 4A, in which the effect size of the interaction is indicated by the differences in the effect of social learning propensity on diet breadth across the three levels of individually initiated learning propensity, and table S4). In general, immatures with high social and individually initiated learning propensities developed broader diet profiles by the onset of independence (Fig. 4A).

Social learning has a compensatory effect on ecological competence development

We found a significant negative effect of the interaction on the estimated breadth of the diet profile at independence [estimate (95% CI) = −36.65 (−70.11, −3.82) food items]. Specifically, the effect of social learning on diet profile breadth was more pronounced when individually initiated learning propensities were low. Among immatures with high individually initiated learning propensities, those who displayed high propensities for social learning had developed diet profiles that were 1.2 times greater than those of immatures who displayed lower social learning propensities (Fig. 4B). Under low propensities of individually initiated learning, the diet profiles of those who displayed high social learning propensities had developed diet profiles that were 1.5 times greater than those who displayed lower social learning propensities (Fig. 4B). Sensitivity analyses by using the three different time thresholds used to extract individually initiated learning events (70, 130, and 160 min) yielded consistent results (tables S5 to S7), indicating robust findings.

Discussion

We leveraged 12 years of long-term data to demonstrate the role that different forms of learning play in the development of a broad and survival-relevant ecological competence in a wild great ape. Our first main finding was that the relative expression of social, socially initiated, and individually initiated learning appear to vary substantially among individuals, as has been shown to be the case in human children (*33*) and both captive (*34*) and wild chimpanzees (*35*). Several factors can lead to individual variation in tendencies to engage in social or individual learning, as well as in learning abilities. Across species, these include genetic differences (*36*), differential developmental influences such as early parental care (*37*), and experienced differences in the reliability of social information (*38*), or a combination of genetic and developmental factors. In orangutans, differences in maternal behavior may be particularly important because offspring-directed behavior is documented to be systematically variable among mothers (*39*).

Whereas studies on other taxa provide mixed evidence for covariation between individuals' experimentally measured immediate social and individual learning abilities or the reliance on such information (*40*–*42*), we found that individuals' natural, average propensities to engage in the three forms of learning over the developmental period did not covary. The absence of a negative correlation between individuals' social and individual learning propensities argues against trade-offs between investment in the two forms of learning and thus against strict individual-specific reliance on a specific form of learning (behavioral specialization) in the wild (*43*).

We found that individual variation was lower in social than individual learning propensities, suggesting that there may be a selection pressure on maintaining rates of social, but not individual, learning above a significant threshold. This may be because individual learning likely carries substantial risks in the wild (*8*). However, the higher individual variation in individual learning propensities as compared with social learning propensities may also partly stem from our choice of an empirically derived cutoff to classify exploration as independent of peering, because we found that the extent of individual variation in individually initiated learning propensity, although substantial, decreased with shorter time cutoffs.

The level of individual variation in social and individual learning propensities observed in this study is unexpected because learning propensities are likely tied to fitness and therefore may have important consequences in this and many other species. 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 (*44*).

Our second major finding was that the commonly made binary distinction between social and individual ("asocial") learning (*45*–*49*) is inadequate in helping us to understand how the development of cultural traits operates in wild animals. In general, peering exerts an influence on exploration for as long as around 2.5 hours in orangutans. We found that the greatest proportion of exploration, in the form of socially initiated learning, is consequent on peering and thus falls at the intersection between social and individual learning. This supports our distinction between what we label here as "socially initiated learning" stimulated by peering within this period—which we accordingly place within the broader conception of social learning (Fig. 5)—and "individually initiated learning" that occurs at other times.

Socially initiated learning occurred at a rate six times greater than individually initiated learning and likely involves selective exploration of the peered-at food item (*23*). It is easy to appreciate that learning through peering alone (what we call "strictly social

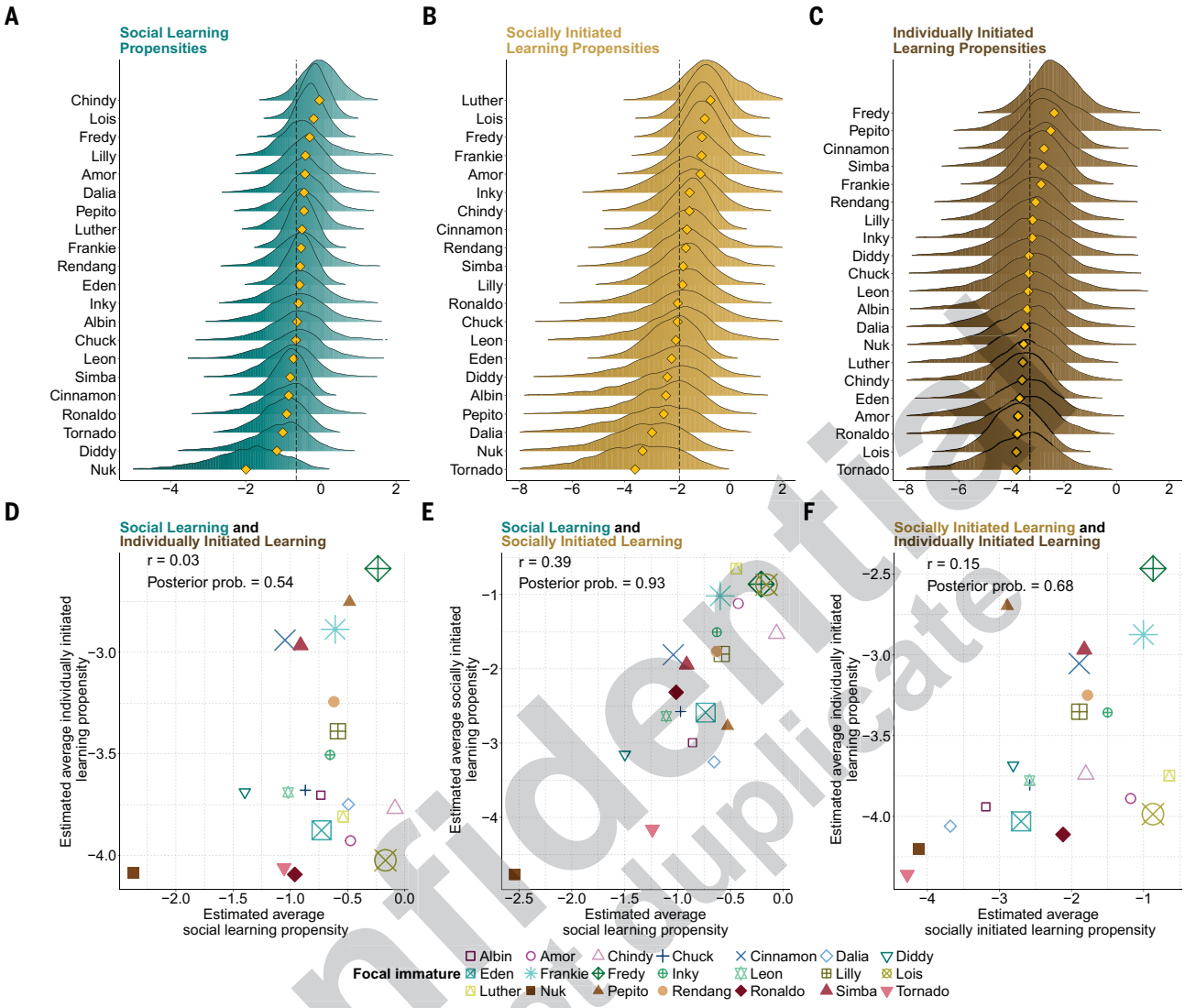

Fig. 3. Individual variation in learning propensities and within-individual relationships between propensities of different forms of learning. (**A** to **C**) Posterior distributions of the estimated average (A) social, (B) socially initiated, and (C) individually initiated learning propensities for 21 immatures over their 8.5-year developmental period. The dashed black line indicates the population average, and the yellow diamond indicates the posterior mean of the estimate for each immature. Values to the left of the dashed line indicate less than population average propensities, and those to the right indicate greater than population average propensities. (**D** to **F**) Scatterplots of individual orangutans' posterior mean for (D) social and individually initiated, (E) social and socially initiated, and (F) socially and individually initiated learning propensities for the 21 immatures. Circle size indicates the total observation duration for each immature between birth and 8.5 years of age ($n = 2$ to 360 hours). Correlation coefficient (r) and posterior probabilities for the hypothesis "$r > 0$" are shown.

learning"), and socially initiated learning may act synergistically in the development of a diet profile. Peering stimulates socially initiated learning and, through effects such as prompting individuals to practice recently observed activities, allows developing individuals to gradually perfect their skills, including complex skills such as tool use (*50*). Our study suggests that during most of the developmental period, immatures engage in both strictly social learning and socially initiated learning, which poses a challenge in estimating their separate effects (an attempt to assess the effect of strictly social learning on diet profile development is provided in fig. S7). Strictly social learning may likely be used by wild orangutans for learning about food items of low preingestive processing intensity such as leaves, which usually involves pick-and-eat techniques (*23*).

Our third and overarching finding is that variation in the totality of social and individual learning propensities that individuals express throughout development shapes the ecological competence that is so critical for the achievement of competent independence. We believe that this constitutes the most important contribution to the field of cultural evolution. Although there are other competencies that a young ape must learn, acquiring ecological competence is likely directly relevant for lifetime fitness and includes the learning of a broad range of skills and knowledge types. At all levels of individually initiated learning, increases in social learning through peering led to greater ecological competence, but the effect of social learning on ecological competence was more pronounced when individually initiated learning was low. This suggests that when immatures do not engage in heightened individual learning to acquire a competence, social learning may compensate for the lack of individual effort. These results reveal how social and individual learning interact to shape diet profile development (Fig. 5).

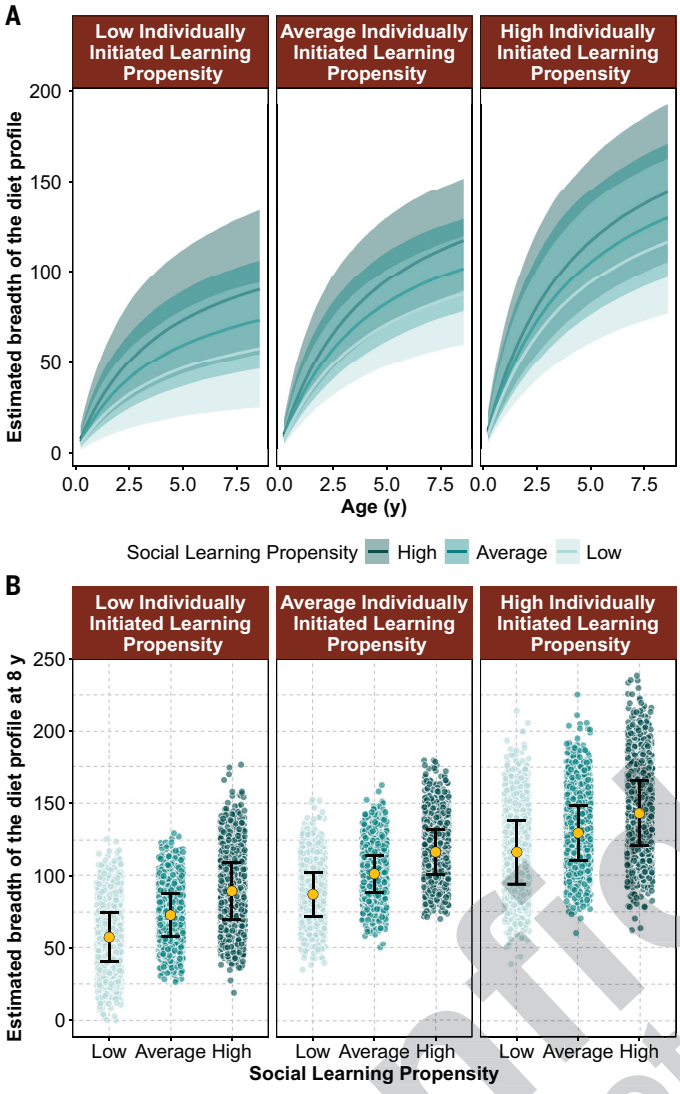

Fig. 4. Predicted effects of social and individual learning propensities on the development of a broad ecological competence. (**A**) Estimated development of the breadths of the diet profiles of immatures between birth and the onset of independence. (**B**) Estimated breadths of the diet profiles at independence, as a function of immatures' estimated average social and individually initiated learning propensities. Low, average, and high refer to mean − 1SD, mean, and mean + 1SD. Each circle indicates a posterior prediction. The yellow circle indicates the posterior mean, and the vertical lines indicate 95% CI.

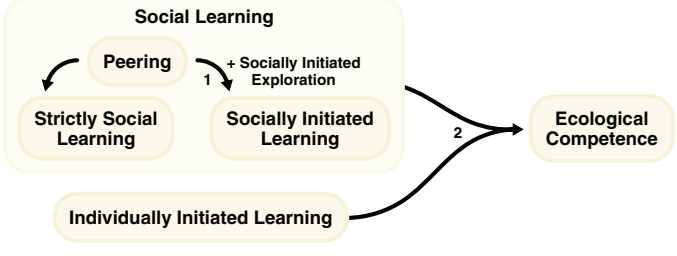

Fig. 5. Overview of the forms of learning involved in diet profile development in Sumatran orangutans. (1) Peering triggers socially initiated learning. (2) Social learning and individually initiated learning interact to influence ecological competence development.

Our study extends our understanding of the pervasiveness of cultural learning in great apes into another dimension, by demonstrating the central role of cultural learning in achieving the extensive diet breadth that sustains great apes' mature, independent foraging. In doing so, we revealed a previously underappreciated interplay between the social and individual components of learning. Our work shows that great ape cultural learning mechanisms are closer to the complexities of the underlying mechanisms of human culture. Because orangutans, the other great apes, and humans share a common ancestry, it is apparent that the extraordinary heights of human cultural learning were likely built on already substantial evolutionary foundations.

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SUPPLEMENTARY MATERIALS

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Materials and Methods; Figs. S1 to S7; Tables S1 to S8; References (*51*–*66*); MDAR Reproducibility Checklist

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