

RESEARCH ARTICLE

Social Learning of Diet and Foraging Skills by Wild Immature Bornean Orangutans: Implications for Culture

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Studies of social learning in the wild are important to complement findings from experiments in captivity. In this field study, immature Bornean orangutans rarely foraged independently but consistently followed their mothers' choices. Their diets were essentially identical to their mothers' even though not all mothers had the same diet. This suggests vertical transmission of diet by enhancement. Also, immatures selectively observed their mothers during extractive foraging, which increased goal-directed practice but not general manipulation of similar objects, suggesting observational forms of learning of complex skills. Teaching was not observed. These results are consistent with the reported presence of food traditions and skill cultures in wild orangutans. We suggest that food traditions can develop wherever association commonly allows for social learning. However, the capacity for observational learning, and thus more complex culture, is more likely to evolve among extractive foragers with prolonged association between adults and immatures. *Am. J. Primatol.* 72:62–71, 2010. © 2009 Wiley-Liss, Inc.

Key words: culture; imitation; orangutans; *Pongo pygmaeus wurmbii*; social learning; teaching; traditions

INTRODUCTION

Traditions [Perry & Manson, 2003] can be operationalized as “behavioral practices that are inherited over generations through social learning.” *Culture* can be defined in different ways [e.g. Galef, 1992; Whiten & van Schaik, 2007] and its presence has been claimed for several animal taxa, including bowerbirds [Madden, 2008], cetaceans [Krützen et al., 2005] and nonhuman primates [Perry & Manson, 2003; van Schaik et al., 2003a; Whiten et al., 1999]. As these claims were based on comparisons of behavioral repertoires between populations while ruling out ecological or genetic factors to explain the differences, we need more direct evidence for social learning in the wild to support claims of culture [Laland & Janik, 2006; van Schaik, 2009]. In the following we adopt social learning definitions as in Whiten [2000]. Convincing evidence for social learning in the wild has been provided by some cleverly designed field experiments [Biro et al., 2003; Reader et al., 2003], but many field studies must rely on purely observational data. How then can social learning be inferred in observational field studies?

Many young animals faced with the challenge of finding food may use social information to optimize their foraging and to avoid potential costs of

individual exploration [Galef & Giraldeau, 2001]. Simple social learning mechanisms such as local or stimulus enhancement (together: enhancement) are widespread in the animal kingdom and generally suffice to explain most instances of social acquisition of diet in nature [ibid.]. For such information transfer to work, immatures merely need to closely associate with experienced conspecifics during foraging, that is “co-forage” [Rapaport & Brown, 2008]. Thus, local enhancement leads to discovery of the same food patches (tree species) and stimulus enhancement to the same items (fruits, leaves) within a patch. In observational field studies, enhancement can be inferred when individuals acquire similar diets as the ones they associate with

Contract grant sponsors: The A. H. Schultz Foundation; The Leakey Foundation; The National Geographic Society; The Netherlands Organization for Scientific Research (NWO).

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Received 14 April 2009; revised 26 August 2009; revision accepted 2 September 2009

DOI 10.1002/ajp.20752

Published online 29 September 2009 in Wiley InterScience (www.interscience.wiley.com).

during foraging [Agostini & Visalberghi, 2005; Schiel & Huber, 2006; Tarnaud, 2004]. If these differ from the diets of other conspecifics for nonecological reasons, they may be called food traditions.

Enhancement allows naïve individuals to learn where or what to eat, but not necessarily how [but see Terkel, 1996]. Thus, it may not suffice in species characterized by cognitively demanding foraging skills not easily discovered individually. Infants may acquire information about difficult-to-process food items through food transfer [Brown et al., 2004]. Furthermore, they may acquire difficult skills, such as tool use, in part through observational learning. Field observations of tool-use development among chimpanzees and capuchins have stressed the importance of observing skilled individuals [Biro et al., 2003; Lonsdorf et al., 2004; Ottoni et al., 2005]. Careful lab experiments, such as those using apparatuses with two distinct solutions and models trained on only one, have confirmed that observational forms of social learning (imitation or emulation) are involved in faithful skill transmission [Dindo et al., 2008; Whiten et al., 2004, 2007]. It is reasonable to assume that similar mechanisms may be at work in the wild for cognitively demanding foraging skills. In observational field studies, their presence could be inferred using two criteria: (1) selective observation of a model for those tasks that are difficult to acquire by individual learning and (2) subsequent goal-directed practice of the same task, using information gained from observation in a way that cannot be explained by enhancement.

The most cognitively demanding foraging tasks may not be acquirable without teaching [Boesch, 1991] and we therefore also looked for behavior fitting the operational definition of teaching among nonhuman animals [Caro & Hauser, 1992].

In this study, we tried to infer the learning mechanisms involved in the acquisition of diet (what to eat?) and foraging skills (how to eat?) by immature Bornean orangutans (*Pongo pygmaeus wurmbii*). Orangutans have been suggested to have cultures [van Schaik et al., 2003a] and are well suited for a developmental study of social learning for several reasons. First, immatures spend years in close association with the mother, even after they begin to move independently at around age three [van Adrichem et al., 2006; van Noordwijk et al., 2009; van Noordwijk & van Schaik, 2005]. Thus, immatures have ample opportunity to learn vertically by enhancement due to the extremely slow life history [Wich et al., 2004] but, at least in Borneo, little or no opportunity to learn from other models due to the semi-solitary life style (<5% association for mothers at Tuanan: van Noordwijk, unpubl. data). Second, orangutans occupy a cognitively demanding foraging niche, including many difficult-to-process items and in some populations tool use [Jaeggi et al., 2008; Russon, 2002; van Schaik et al., 1996], the

acquisition of which may require more sophisticated learning mechanisms such as imitation [Russon & Galdikas, 1993].

In sum, we infer (1) social transmission of diet (what to eat) by enhancement, if immatures (a) co-forage with their mothers rather than independently, (b) rarely try novel foods, and (c) eat the same food items as their mothers even though the mothers' diets may differ for no ecological reason, indicating that other food is available. Furthermore, we infer (2) observational learning of foraging skills (how to eat), if immatures (a) selectively observe the mother during difficult tasks and (b) subsequently practice these skills in a goal-directed way, thus ruling out enhancement. Finally, we predict that (3) teaching will be restricted to the most difficult skills.

METHODS

Subjects and Data Collection

This study was conducted at the Tuanan field station (2°09'S, 114°26'E) in the Mawas Reserve, Central Kalimantan, Indonesia [van Schaik et al., 2005]. Focal animals were followed from their morning to their night nest for at most 10 consecutive days. Offspring ages were estimated at the onset of continuous research in 2003 based on body size and locomotor skills and subsequently fine-tuned by using time series of photographs. One offspring, KON, was weaned shortly before the start of this study. The activity of both mother and offspring was recorded instantaneously every 2 min [Martin & Bateson, 1993] using a standardized protocol (www.aim.uzh.ch/orangutannetwork.html). All social interactions were carefully described in the field and later coded for analysis by A. J. Detailed observations on rates of food interactions, that is solicitation and watching, were made from March to September 2005 totaling 1145 observation hours [see Jaeggi et al., 2008 for solicitation and sharing rates]. In addition, data collected in 2006 were used for co-foraging patterns, including one more subject born February 10, 2006 and totaling another 813 hr of observation (see Table I). Observers were students from the universities of Jakarta (UNAS), Utrecht and Zurich as well as trained local assistants. On any given follow at least two observers were present. Jaeggi et al. [2008] provide details on inter-observer reliability.

Definitions

A *feeding bout* is continuous feeding on the same item in the same patch. Different items (fruits, flowers, leaves, etc.) of the same plant species were counted as distinct *food items*. Following Parker and Gibson [1977], items were divided into embedded and nonembedded food. *Embedded* items are pith, inner bark (phloem and cambium), social insects

TABLE I. Details on Subjects and Observation Times

Mother	Offspring	(Est.) Birth ^a	2005			2006		
			Days	Hours	FBs ^b	Days	Hours	FBs
JUN	JIP, m	February 10, 2006				13	124	284
JIN	JER, m	I 2003	35	339	516	15	225	394
SUM	SUS, f	II 2002	14	236	216	14	152	261
MIN	MIL, f	II 2001	26	345	571	16	175	326
KER	KON, f	II 1999	22	225	640	13	137	371
Total			97	1145	1943	71	813	1636

^aI: first half of year; II: second half of year.

^bFBs: Feeding bouts.

(ants, bees, termites) in nests and seeds of those fruits that require additional processing after opening the shell. *Nonembedded* items are all other fruits, flowers and leaves. Food items were divided into *high* or *low quality* and *difficult* or *easy* as in Jaeggi et al. [2008]. *Food solicitation* is any attempt by the infant to take food from the mother. *Watching* was recorded whenever the offspring looked at the mother from close distance (<2 m) for at least 5 sec, without soliciting food, while the mother was feeding, that is procuring, processing or eating food. *Trying of food* refers to feeding attempts on novel items without ingestion. An item was considered *novel* if it was never recorded as eaten before and an item was considered part of an individual's diet if it was eaten on more than one occasion or during more than one 2-minute scan [Bastian et al., 2009]. *Practice* is a goal-directed but unsuccessful attempt at procuring or processing an item. *Object play*, on the other hand, is playful handling of any object without apparent feeding purpose. *Co-foraging* is feeding in the same patch and on the same item. *Teaching* was defined as by Caro and Hauser [1992].

Analysis

Diet and home-range overlap

All food items eaten in the period from March to September 2005 for more than two 2-minute scans were compared. Items eaten by only one individual were still counted as eaten by both if the other had eaten it before the study period. The overlap was calculated as the percentage of items eaten by both from among all items eaten by the two combined. The mean (\pm SD) number of days between follows on different females in the study period was 9.9 (\pm 10.3) days. As an indicator of similar food availability we used the core home-range overlap of the females, defined as the area in which they spent 50% of their time, calculated using digitized 30-minute records of each focal animal's location with ArcView 9.x by Wartmann [2008]. The mean core home-range overlap was 15.5% (\pm 6.3). In addition, for the two females with the most overlapping core area (JIN and SUM, 25.1%) diet overlap was calculated again using

stricter criteria: To control for (1) temporal variation in food availability, follows in a calendar month during which the other mother was not sampled were excluded; and to control for (2) spatial variation in food availability, only follows were included when they ranged within 200 m of the other's location in the same month. Thus, 20 and 17 follow days, respectively, were used. The mean number of days between follows on these two mothers thus compared was 9.3 (\pm 4.4) days. Hence, the same food items were potentially available to these females.

Diet overlap was compared using Mann-Whitney *U* tests in SPSS 17.0. *P*-values are two tailed unless otherwise indicated. Exact *P*-values are reported to avoid incorrect values for small sample sizes [Mundry & Fischer, 1998]. A hierarchical cluster analysis on diet similarity was performed on 85 food items eaten by at least one individual using the complete agglomerative nesting method with manhattan metric in the "cluster" package [Maechler et al., 2005] for R 2.9.0. [2009].

Watching rates

Watching rates were calculated for each food item eaten by a female as the proportion of maternal feeding bouts in which watching by the offspring occurred at least once. We also calculated a stricter watching rate, excluding the possibility that watching was related to food solicitation, as the proportion of maternal feeding bouts in which watching *but no food solicitation* occurred. The influence of the factors "embedded/nonembedded," "high/low quality" and "difficult/easy" on watching rates was analyzed by fitting generalized linear mixed effect models [GLMM's, Bolker et al., 2009], with quasi-binomial error distribution and logit link function using the LME4 package [Bates et al., 2008] for R 2.9.0 [2009]. Average feeding bout lengths (\pm SD) were not significantly different neither for embedded vs. nonembedded items (13.1 \pm 12.2 vs. 15.9 \pm 17.6 min, $t_{203} = -0.69$, $P = 0.49$) nor for difficult vs. easy items (17.7 \pm 18.5 vs. 13.7 \pm 17.6, $t_{188} = 1.57$, $P = 0.12$), thus allowing for equal watching opportunities. Lengths did differ though for high- vs. low-quality items (18.6 \pm 18.4 vs. 7.6 \pm 9.7, $t_{203} = 4.25$,

$P < 0.001$), suggesting that higher watching rates for high-quality items may simply be due to longer opportunities for watching. GLMM's were weighted by the total number of feeding bouts on each food item to control for sampling bias and subject ID was included as a random factor to control for variation among the immatures. Different GLMM's were fitted using each of the three factors separately or in any combination, with or without interaction effects. No interaction effect could be modeled for embedded*difficult, because embedded was almost a subset of difficult. The different GLMM's were then compared for the amount of variance explained to select the model with the best fit to the data [Crawley, 2005; McCullagh & Nelder, 1989]. F -statistics and P -values from GLMM's were calculated following Faraway [2006 and changes thereto].

Practice and object play

The distribution of practice and object play with dead wood by two immatures within the three time periods 1 hr before the start of termite feeding, 1 hr after this, and all remaining observation time was compared using χ^2 "goodness of fit" tests. We tested for the contingency of practice and object play, respectively, on watching or food solicitation during the previous feeding bout, by comparing their frequency after feeding bouts with interactions to feeding bout without interactions using the same tests. As the numbers for this analysis were very small, we report the corrected χ^2 value and the cumulative estimated P -value after a Monte Carlo Simulation with 10 000 random samples.

This research adhered to the legal requirements of Indonesia and was approved by the Indonesian Institute of Science (LIPI).

Results

Social Transmission of Diet (What to Eat)

Co-foraging

Immatures up to weaning age co-foraged with their mother in the great majority, about 90%, of their feeding bouts, and only rarely foraged independently (Fig. 1). In contrast, the one weaned subject foraged more independently, but still largely on the same food items. Hence 94% of the unweaned offspring's feeding time (425 hr) was when the mother was also feeding, and to over 96% on the same food items. Thus, infants up to at least 4 years of age in this population foraged mostly together with the mother and only the one weaned immature foraged more independently.

Independent exploration

Offspring ate an average of 3.5 food items that were not recorded to be eaten by their mothers, that is 5.9% of their dietary repertoire. However, there

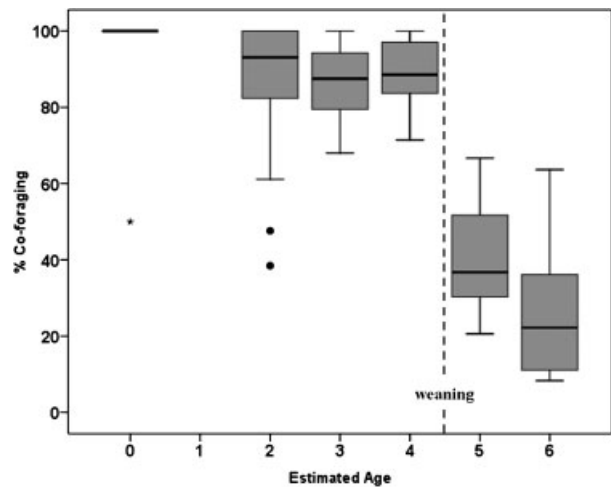


Fig. 1. The percentage of feeding bouts by the offspring that were co-foraged, that is feeding in the same patch as the mother, ranked in order of (estimated) age. Boxplots represent the median and quartiles. Age classes 2 and 3 include two and three subjects, respectively, whereas all other age classes include only one subject each (see Table I). Based on a total of 3,579 feeding bouts with full follow days as units ($n = 168$).

were only 18 feeding bouts on such items, as compared with 1925 feeding bouts on food items that were also eaten by the respective mother, that is less than 1% of the offspring's feeding bouts or 0.5% of their total feeding time (634 hr). In addition, all offspring combined tried novel food 10 times, but none of these food items were ever fully eaten, tried again or consequently included in any offspring's diet. Hence, it seems that items not eaten by the mothers are hardly ever eaten, and individual exploration rarely involved trying novel food.

Diet composition

High diet overlap between mother-offspring pairs could reflect social learning, if other food was potentially available. To test the latter, we compared diet overlap among mothers with their home-range overlap. If diet overlap among mothers was independent of home-range overlap this suggests differential selection among all potentially available food items, despite similar availability. Furthermore, diet overlap among mothers could also reflect (past or present) opportunities for social learning, if it is related to association patterns. For this purpose, we used a natural transplantation experiment: the female SUM moved to the study site after most of her former home range had been lost to forest fires. She never associated with the other "resident" females, despite sharing increasing parts of her home range with them. On the other hand, the resident females are known to be maternal relatives (Arora, in preparation) and regularly associated. Hence, we expected differences in diet between the cluster of resident females and SUM.

On average 55.5 items were eaten by both mother and offspring in this period, whereas 3 and 3.5 items were eaten only by the mother or only the offspring, respectively. Hence the overlap between mother and offspring averaged $89.5\% \pm 2.9$ SD (Fig. 2), significantly higher than the average overlap among the mothers ($77.6\% \pm 7.4$ SD, Mann-Whitney U test: $n_1 = 4$, $n_2 = 6$, $Z = 2.56$, $P = 0.01$). Diet overlap among mothers was not significantly correlated with core home-range overlap (Spearman's $r_s = 0.66$, $N = 6$, $P = 0.16$). Likewise, diet overlap among immatures was not significantly correlated with core home-range overlap of the mothers ($r_s = 0.14$, $N = 6$, $P = 0.79$).

As expected, all females showed the lowest overlap with SUM (mean involving SUM = $71.0\% \pm 2.0$ SD, mean among resident females = $84.2\% \pm 0.5$ SD, MWU: $n_1 = 3$, $n_2 = 3$, $Z = 1.96$, $P = 0.05$ (one tailed), Fig. 2), and all immatures showed the lowest overlap with SUM's daughter SUS ($51.8\% \pm 1.2$ SD vs. $84.3\% \pm 2.1$ SD, MWU: $n_1 = 3$, $n_2 = 3$, $Z = 1.96$, $P = 0.05$ (one tailed), Fig. 2), even though there was no part of SUM's home range that was not used by other females during the period considered here. This result is robust, because the diet overlap between SUM and JIN (who had the highest core home-range overlap) measured when they foraged in the same area in the same period, was still lower than that among all the other females (79.2 vs. $84.2\% \pm 0.5$ SD). Furthermore, a hierarchical cluster analysis of diet composition confirmed that SUM and SUS cluster on their own, whereas the residents cluster together. The height difference between the "resident" and "immigrant" clusters was more than half of the total tree height. Among

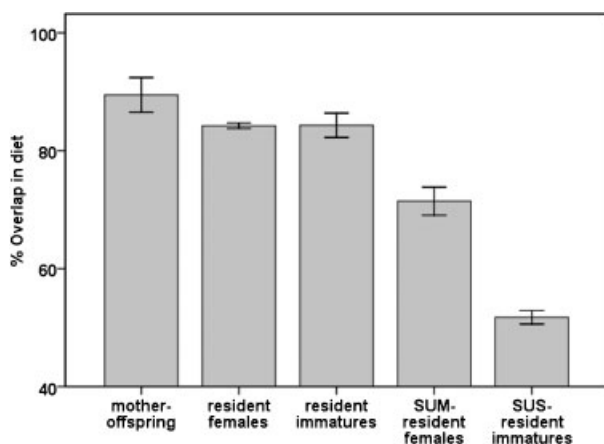


Fig. 2. Diet overlaps (\pm SD) between mothers and offspring, the three "resident females" belonging to the same matriline, their offspring ("resident immatures"), the "immigrant" female SUM and the resident females and SUM's daughter SUS and the resident immatures. Clearly, all offspring followed their mothers' choices, whereas SUM ate different food items than the other females and her daughter SUS ate different food items than the other immatures. SUM originally came from a different area and never associated with the resident females.

the residents, mother-offspring pairs cluster together, with the exception of JIN and JER. On average, items eaten by one female but not another accounted for $2.29 \pm 2.5\%$ of the total feeding time. This percentage was significantly higher for dyads including SUM ($3.9 \pm 2.6\%$) than among the resident females ($0.66 \pm 0.66\%$; $t_{10} = 2.94$, $P < 0.05$).

These results suggest that (i) offspring inherited the diet of their mothers through social learning because the mothers' diets did not include all potential food items, and that (ii) diet overlap among mothers also reflect opportunities for social learning, as shown by the natural transplantation experiment of the immigrant SUM.

Observational Learning of Extractive Foraging (How to Eat)

Selective observation

There were 65 instances of watching on 16 different food items. The GLMM explaining most of the variance in watching rates was the full model, including all three factors. However, the factor embedded/nonembedded alone explained most of the variance ($F_{1,200} = 481.1$, $P < 0.001$, Fig. 3). The interaction effect of embedded*high ($F_{1,200} = 45.27$, $P < 0.001$) as well as the factors high/low quality ($F_{1,200} = 43.18$, $P < 0.001$) and difficult/easy ($F_{1,200} = 5.96$, $P < 0.05$) also had significant but much smaller influences. The random factor individual had zero variance, indicating that all immatures behaved in the same way. Running the same model again but using the stricter definition of watching rate (excluding bouts with food solicitation) yielded the same results (embedded: $F_{1,200} = 404.3$, $P < 0.001$; high quality: $F_{1,200} = 119.2$, $P < 0.001$; embedded*high quality: $F_{1,200} = 73.7$, $P < 0.001$; difficult: $F_{1,200} = 7.1$, $P < 0.01$). As embedded had such a major influence and the factors were not entirely independent, the significance of the other factors could just

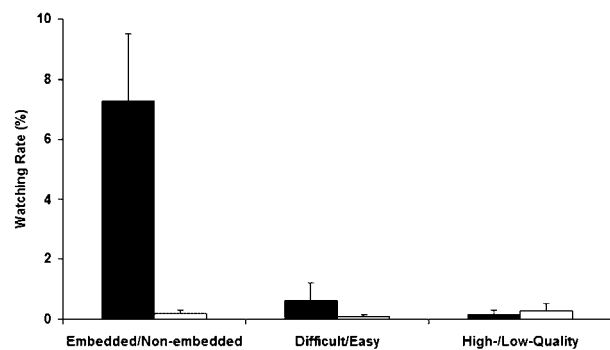


Fig. 3. Mean watching rates (\pm SEM) for embedded/non-embedded, (nonembedded) difficult/easy as well as (non-embedded) high-/low-quality food items. Watching rates were calculated as the percentage of feeding bouts by the mother during which the offspring closely observed the mother without soliciting food. Watching rates were significantly higher for embedded items, but not for (nonembedded) difficult or high-quality food.

be driven by embedded–difficult and embedded–high-quality items. Hence, we fitted another model with difficult/easy and high/low quality as factors including only nonembedded items (Fig. 3). In this model, difficulty still had a significant influence on watching rates ($F_{1,165} = 15.7, P < 0.001$), but neither quality ($F_{1,165} = 0.15, P = 0.7$) nor the interaction difficulty*quality ($F_{1,165} = 0, P = 1$) did. If these nonsignificant factors are further removed from the model, the effect of difficulty also disappeared ($F_{1,167} = 0.17, P = 0.7$). The same results were found using the stricter definition of watching rates (*Model with both factors*: difficulty: $F_{1,165} = 11.7, P < 0.001$; quality: $F_{1,165} = 0.01, P = 0.9$; difficulty*quality: $F_{1,165} = 0, P = 1$; *Model with only difficulty*: $F_{1,167} = 0, P = 1$).

Practice

Orangutans at Tuanan eat termites out of nests hidden in dead wood by biting it open and sucking them out. Even adults have difficulties locating such nests and immatures sometimes practiced this foraging method by biting open dead wood and looking at the opened patches just as if foraging for termites. Playing with dead wood on the other hand did not involve such goal-directed behavior. We compared the occurrence of practice and object play throughout the day and in particular in the 1-hour period before and after the start of a mother's feeding bout on termites ($N = 80$). We propose that (i) if the behaviors are equally distributed, they are not related to external stimuli, (ii) if they are restricted to the termite foraging context, they are related to environmental stimuli such as availability of dead wood, (iii) if they are increased after the mother's termite foraging they are enhanced by social stimuli (stimulus enhancement), (iv) if goal-directed practice is increased more than non-functional playing by these social stimuli, then observational forms of learning could be responsible, in particular (v) if goal-directed practice is contingent on previous interactions such as watching and/or food solicitation, but playing is not.

There were 19 well-described cases of “termite foraging practice” by two different immatures, JER and MIL. Three observations of practice fell into the 1-hour period before the start of a mother's feeding bout on termites (i.e. 3 in 80 hr), 13 into the period afterwards (13/80 hr) and three fell outside both of these periods (3/524 hr). This distribution was not different for the two immatures (Fisher's exact probability: $P = 1.0$), hence the data were pooled. (i) Practice was distributed significantly differently than expected by chance throughout the observation time (Goodness of fit: $\chi^2 = 61.7, df = 2, P < 0.0001$, Fig. 4), suggesting the possibility of environmental and social effects. In particular, (ii) both the amount of practice within 1 hr after termite feeding and 1 hr

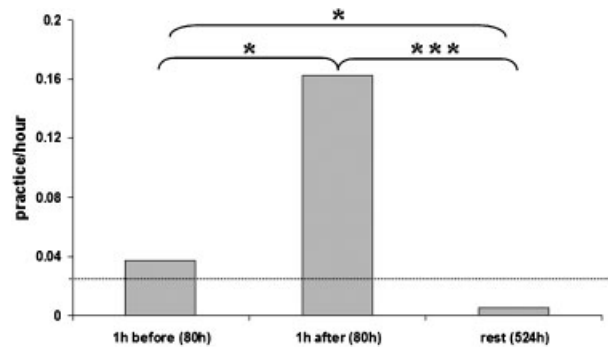


Fig. 4. Rates of termite foraging practice per hour, for the time periods within one hour before (“1 hr before”) and one hour after the start of a mother's feeding bout on termites (“1 hr after”) as well as during the rest of the observation time (“rest”). The dashed line represents the average rate per hour. The increase after a mother's feeding bout suggests a social effect on practice. *** = $P < 0.001$, * = $P < 0.05$.

before termite feeding were significantly different from the rest of the observation period ($\chi^2 = 58.58, df = 1, P < 0.0001$; $\chi^2 = 4.17, df = 1, P < 0.05$, Fig. 4), suggesting some environmental effect. Furthermore, (iii/iv) practice occurred significantly more often within 1 hr after the start of a maternal feeding bout on termites compared with 1 hr before ($\chi^2 = 6.25, df = 1, P < 0.05$, Fig. 4), suggesting a social effect. Finally, (v) was this increase contingent on interactions during the previous feeding bout? For one immature, JER, there was a clear trend in that all instances of practice occurred after feeding bouts with interactions (Interaction Bout “IB”) and none after feeding bouts without interactions (“NIB”): 7 vs. 0, 18 IB, 9 NIB, “Goodness of fit”: corrected $\chi^2 = 2.16$, cumulative estimated probability after 10,000 random samples $P = 0.1$. This trend is consistent with observational learning. For the other immature MIL there was no such trend (4 vs. 2, 33 IB, 20 NIB, $\chi^2 = 0, P = 1$).

There were 56 cases of playing with dead wood by the same subjects, 5 and 10 of which, respectively, fell into the period 1 hr before and after a termite feeding bout, whereas 41 fell outside both of these periods (5/80, 10/80, 41/524 hr). Again, the distribution was not different for the two immatures (Fisher's test: $P = 1.0$), allowing data to be pooled. (i) Playing was not distributed differently than expected throughout the observation time ($\chi^2 = 2.27, df = 2, P = 0.32$), suggesting no relation to external stimuli. There was (ii) no significant difference between 1 hr after and 1 hr before a feeding bout compared with the rest of the observation period, respectively, ($\chi^2 = 1.29, df = 1, P = 0.26$; $\chi^2 = 0.07, df = 1, P = 0.79$), suggesting no environmental effect and (iii/iv) no significant increase in object play within 1 hr after the start of a maternal feeding bout compared with 1 hr before ($\chi^2 = 1.67, df = 1, P = 0.3$), suggesting no social effect. (v) playing after termite feeding bouts was not contingent on

previous interactions for one immature (JER 3 vs. 1, 18 IB, 9 NIB, $\chi^2 = 0$, $P = 1$) and there was even a trend in the opposite direction for the other (MIL 1 vs. 5, 33 IB, 20 NIB, $\chi^2 = 3.56$, $P = 0.09$). This suggests that general handling of dead wood was not increased by observation, or even decreased.

Thus, (i) practice but not playing seemed related to external stimuli, in particular (ii) environmental and (iii) social ones. Furthermore, (iv) goal-directed practice was increased more than nonfunctional playing by social stimuli, indicating that observational learning may have focused the immatures learning attempts to the relevant tasks. Finally, (v) a contingency on previous interactions such as watching and/or food solicitation could be shown for one immature.

Teaching

We found no evidence of either (i) opportunity teaching, (ii) coaching or (iii) active teaching as mothers (i) never changed their own behavior in order to put their offspring in a position to learn, (ii) neither discouraged nor encouraged intake of food and (iii) never actively assisted their offspring's feeding attempts in any way.

DISCUSSION

We evaluated a number of predictions to test whether immature orangutans acquired feeding-related knowledge by learning socially from the mother or independently, and whether observational forms of learning were involved in the acquisition of cognitively more demanding foraging skills. Unweaned immatures mainly co-foraged with their mothers, spending the vast majority of their feeding time near their mother, rather than alone (Fig. 1). The drastic decline in co-foraging for the one weaned subject may be explained by the fact that the mother was being consorted by males during most of the study period and that there were signs of parent-offspring conflict, both of which led to increased distance between the two [Jaeggi et al., 2008]. However, the offspring still ate largely the same items, following the mother to food sources and diet overlap only slightly decreased over time [Latscha, 2008]. Immatures did eat a few items not eaten by their mothers, but such sampling of novel foods was rare and seldom repeated. Similar to some other primates [Krakauer & van Schaik, 2005; Ueno & Matsuzawa, 2005; Voelkl et al., 2006], immatures referred to the mother before ingesting novel food items, even if they were easily processed and readily available (e.g. MIL watching and soliciting from MIN eating flowers of *Garcinia bancana*). This indicates that immatures mainly relied on the mother to find and identify edible food items, if they could.

The immatures' dietary repertoire was essentially identical to their mothers', whereas the diets of

adult females differed significantly (Fig. 2). However, diet overlap among females was not related to similar food availability, as it did not correlate significantly with core home-range overlap. Instead, the natural transplantation experiment of the immigrant SUM showed that diet selection varies according to the predicted patterns of different (geographical and genetic) origin and (past and present) association. SUM clearly had a different diet from all other females, even though her home range lay within the others' ranges, and even when she foraged in the same area at the same time. SUM's daughter SUS also clearly had a different diet from all other immatures, thus indicating that she had inherited the "foreign" diet of her mother. This pattern was confirmed by a hierarchical cluster analysis. In sum, immatures mainly co-foraged with their mother and ate the same food items, even though other edible items were available, suggesting vertical transmission of food knowledge by social learning.

Cognitively more demanding foraging skills may have to be acquired by other forms of social learning and subsequent practice. All immatures observed the mother more often when processing embedded food (Fig. 3). Watching rates were comparable to those reported for *Coula* nut cracking among Tai chimpanzees for similarly aged offspring [Boesch & Boesch-Achermann, 2000]. Embedded food items require extractive processing and may be hard to find (insects), seemingly unpalatable (some fruits) and/or not easily recognizable as food (inner bark, pith). Thus, repeated observation may be necessary to learn how to recognize and process such food items. Despite the significant interaction with food quality, observation was not related to food solicitation, as the results did not differ when bouts with food solicitations were excluded. Other difficult items such as tough-shelled fruits only rarely increased visual attention (Fig. 3), which can be explained by the fact that they were hard for immatures to open for lack of strength, but in principle simple to recognize and to process. Thus observation seems to be specific to those food items that are hard to find and require extractive processing, that is those skills that are not easily learned independently.

To test whether immatures put the information gained from social stimuli into practice, we compared the occurrence of termite foraging practice and playing with dead wood. Exposure to the mother's termite foraging significantly increased the immatures' goal-directed practice of the same task (Fig. 4), but not general manipulation of similar objects, that is playing with dead wood. The slight increase in playing, which may become significant in a larger sample, indicates that stimulus enhancement may explain some of this increase. However, the fact that goal-directed practice was increased more than nonfunctional playing hints at observational forms of learning, allowing the offspring to focus their

attempts on the relevant tasks. A contingency of practice on watching and/or food solicitation during the previous feeding bout could be shown for one immature. Although these results have to be interpreted with caution due to the small number of observations, they are consistent with observational learning. Furthermore, the same selectivity of watching and a contingency of practice on previous watching has now been demonstrated in another population [Forss, 2009]. In sum, the combined evidence of selective watching and subsequent goal-directed practice, possibly contingent on previous social interactions, suggests observational forms of learning beyond enhancement for some extractive foraging skills.

Teaching was never observed in over 1,000 observation hours, suggesting that mothers only rarely, if ever actively support their offspring's learning in the context of food selection or foraging skills in this population. This is consistent with studies on skill development in chimpanzees, which mostly report a passive role of the mother [Hirata & Celli, 2003; Lonsdorf, 2006; Matsuzawa et al., 2001]. Only the most difficult or dangerous skills may require some teaching [Boesch, 1991; Humle, 2009].

Our results necessarily suffer from the constraints of small sample size but are nonetheless consistent with other work. Rijksen [1978] showed that adult orangutans were novelty averse and only ate novel food if they saw a con-specific do so. Rehabilitant orangutans are slow to expand their diet breadth by independent exploration but eager to learn from others [Russon, 2002, 2006]. This suggests that orangutans rely on social information to find food, if they have a choice. Taken together, the picture emerges of orangutans as preferably relying on (i) social information to acquire the main bulk of their diet, (ii) food transfers to learn about the composition of difficult-to-process items [Jaeggi et al., 2008], and (iii) an interplay of observation and practice to acquire some extractive foraging skills. Further studies at other sites seem to confirm this [Forss, 2009]. Although individual learning may become more important for independent juveniles, a general reliance on social learning could explain some differences in diet and feeding techniques found within and between sites [Bastian et al., 2009; van Schaik et al., 2003b; van Schaik & Knott, 2001] and the development of different cultures in orangutans [van Schaik et al., 2003a].

The results of this study provide suggestions for the conditions in which to expect food traditions and foraging skill cultures among other animals. Young animals should prefer social information to focus their foraging and to avoid the risks and difficulties of independent exploration [Galef & Giraldeau, 2001; van der Post & Hogeweg, 2006], but their opportunities to do so might vary across taxa. Immatures of species with slow-paced life histories, spending more

time in close association with parents or caregivers, engage less in independent exploration, as social influences on learning are unavoidable [Elephants: Lee & Moss, 1999; Dolphins: Mann & Sargeant, 2003; Primates: Rapaport & Brown, 2008]. Thus, these are also the taxa in which we expect food traditions, if diet breadth allows for individual variation.

Additional forms of social learning may be necessary to learn how to process food items when this is not easily discovered individually, in the form of food transfers [Brown et al., 2004] or through selective observation [Biro et al., 2003; Lonsdorf et al., 2004; Ottoni et al., 2005; Perry & Ordóñez Jimenez, 2006]. In the wild, selective observation alternating with practice may go on for years before immatures fully master the cognitively most demanding skills [Boesch & Boesch-Achermann, 2000; Lonsdorf et al., 2004; Matsuzawa et al., 2001]. Similar patterns may be present in cetaceans and elephants [Boran & Heimlich, 1999; Lee & Moss, 1999]. Thus, we suggest that species relying on cognitively demanding foraging skills need to use observational forms of learning and are thus more likely to develop culture *sensu* Galef [1992]. Regular teaching may evolve only where the benefits to the pupil, and hence indirectly to the teacher, are unusually large [Thornton & Raihani, 2008], as in cooperative breeders [Burkart et al., 2009; van Schaik & Burkart, 2009].

In conclusion we suggest that (1) prolonged close association and high tolerance between adults and immatures may lead to suppressed independent exploration and thus the development of food traditions due to social learning of diet [Galef & Giraldeau, 2001], and that (2) a reliance on cognitively demanding foraging skills favors the evolution of observational learning [Byrne, 2007] and thus culture *sensu* Galef [1992].

ACKNOWLEDGMENTS

We are grateful to the Director General at PHKA, T. Mitra Setia and S. S. Utami-Atmoko of the Universitas Nasional Jakarta, BKSDA Palangkaraya, the directors and staff of BOS-Mawas, the Departamen Dalam Negeri and LIPI for supporting our research in Indonesia. We thank all the students and local assistants who helped with the data collection and E. R. Vogel for help and support in the field. Research at Tuanan was financially supported by the A. H. Schultz Foundation, the Leakey Foundation, the National Geographic Society and the Netherlands Organization for Scientific Research (NWO). Finally, we thank F. Wartmann for assistance with ArcView, and G. Anzenberger, M. Bastian, J. M. Burkart, K. Isler and M. Krützen for comments and discussion. This research complied with the animal care regulations and national laws of Indonesia.

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