



Observational social learning and socially induced practice of routine skills in immature wild orang-utans



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Experiments have shown that captive great apes are capable of observational learning, and patterns of cultural variation between populations suggest that they use this capacity in the wild. So far, the contexts and extent of observational forms of social learning in the wild remain unclear. Social learning is expected to be most pronounced during the skill acquisition of immature individuals. We therefore examined peering (attentive close range watching) by immatures in two populations of wild orang-utans, *Pongo* spp. We found, first, that peering was most frequent in contexts in which learning is expected, namely feeding and nest building. Second, peering in the feeding context was significantly positively correlated with complexity of food processing and negatively with an item's frequency in the mother's diet. Food peering was also followed by significantly increased rates of exploratory behaviours targeting the same food items, indicating that it leads to selective practice. Food peering also decreased with age and increasing feeding competence of the immatures. Third, the age of peak peering in the nesting context coincided with the onset of nest practice behaviour, and peering events were followed by significantly increased rates of this behaviour. Fourth, the proportion of peering directed at other individuals rather than the mother increased with age. These findings are consistent with the prediction that immature orang-utans learn by observing others in a variety of contexts and that peering is followed by selective practice of the observed behaviour. We conclude that observational social learning in combination with socially induced practice over a period of several years is a critical component of the acquisition of learned subsistence skills in orang-utans.

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Social learning is learning that is influenced by observing, associating with or interacting with individuals or their products (Heyes, 2012). It is the necessary precondition for the emergence and maintenance of traditions and cultures (van Schaik et al., 2003; Whiten et al., 1999). Also, since the ability to learn socially from others makes learning more efficient, it might be the driving force behind the evolution of intelligence (Reader & Laland, 2002; van Schaik & Burkart, 2011). The simplest forms of social learning are nonobservational. This includes social facilitation and local enhancement, where learning is based on the mere presence of conspecifics or their interaction with a specific object at a specific site and thus not dependent on observing the actions of conspecifics. Evidence for nonobservational forms of social learning has

been found in several fish, reptile, bird and mammal species, which suggests deep evolutionary roots (reviewed by Galef & Laland, 2005; Rapaport & Brown, 2008; Reader & Biro, 2010). However, the effective transmission of knowledge, such as complex food-processing techniques (e.g. tool use), may require more efficient and accurate forms of social learning, such as observational social learning. Observational social learning (learning by observing others) includes some forms of stimulus enhancement as well as imitation, emulation or observational conditioning (Hoppitt & Laland, 2013; Tomasello, 1994; van Schaik, 2010). Several authors have also pointed out that for many detailed actions competence can only be acquired by individual practice (Byrne & Russon, 1998; Galef, 2015), suggesting that observational learning will often need to be accompanied by selective practice.

Communities and populations of chimpanzees, *Pan troglodytes*, and local populations of orang-utans, *Pongo* spp., show behavioural variation that cannot be explained by environmental or genetic differences (Kruetzen, Willems, & van Schaik, 2011; Whiten et al.,

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1999; Whiten & van Schaik, 2007). Less extensive variation in individual behavioural elements has also been found in wild populations in a variety of primate, bird and cetacean species (reviewed by Frigaszy & Perry, 2003; Galef, 2004; Whiten, 2012). Each of these studies concluded that social transmission best explains the observed patterns of behavioural variation. Diffusion patterns documented for experimentally introduced knowledge or, in a few cases, newly acquired behavioural variants in the wild are highly suggestive of the operation of social learning in the wild (e.g. Hobaiter, Poisot, Zuberbuehler, Hoppitt, & Gruber, 2014; van de Waal, Krutzen, Hula, Goudet, & Bshary, 2012; reviewed by Reader & Biro, 2010; van Schaik, 2003; Whiten & Mesoudi, 2008). Likewise, studies relating behavioural similarity within groups to association patterns are also consistent with social transmission (Matthews, 2009; Perry, 2009).

Most field studies could not identify the mechanism of social learning at work since they only looked at the results of social learning and not at the process itself. Moreover, they mainly focused on innovative behaviours (e.g. complex feeding techniques or social interactions), which show geographical variation between populations or groups and thus could be most reliably identified as being socially learned. Noninnovative behaviours tend to be more common and do not necessarily result in population differences (Hoppitt, Samson, Laland, & Thornton, 2012; Thornton & Malapert, 2009). However, it is unlikely that the mechanisms of social learning only evolved for the rare case of transmitting novel behaviour. The more likely scenario is that social learning evolved in the context of routine skill acquisition (such as basic feeding skills) by immatures. This important idea has so far not been systematically investigated.

Experiments on captive primates have elucidated the social learning mechanisms of which a species is capable (reviewed by Whiten & Mesoudi, 2008; Whiten, 2012). Using the two-action paradigm approach (Dawson & Foss, 1965; Whiten & Cusance, 1996) numerous studies on a variety of species have successfully distinguished between nonobservational and observational forms of social learning. This approach has demonstrated observational learning under experimental conditions in chimpanzees (e.g. Hopper et al., 2007; Whiten et al., 2007), gorillas, *Gorilla gorilla gorilla* (Stoinski, Wrate, Ure, & Whiten, 2001) and orang-utans (Dindo, Stoinski, & Whiten, 2011; Russon & Galdikas, 1993; Stoinski & Whiten, 2003). Evidence for observational learning has also been found in a few monkey and several bird species (reviewed by Whiten & Mesoudi, 2008; Whiten, 2012; Zentall, 2011).

Important as they are, these studies cannot tell us whether and in what contexts species rely on observational learning as a means of skill acquisition under natural conditions (Reader & Biro, 2010). Most experiments are of extremely short duration relative to the long developmental period of most primates and the time needed in the wild to acquire subsistence skills (e.g. Lonsdorf, 2006). On the other hand, in captivity, many species show behaviours that are significantly more complex than they do in the wild (Benson-Amram, Weldele, & Holekamp, 2013; Forss, Schuppli, Haiden, Zweifel, & Van Schaik, 2015; Kummer & Goodall, 1985). Also, species that show social learning in captivity may fail to do so in the wild (Gajdon, Fijn, & Huber, 2004, 2006).

Unfortunately, field experiments are difficult to conduct and ethically sensitive. This is why to-date few field experiments on social learning in primates have been conducted. Mostly based on the two-action paradigm, field experiments have produced evidence for forms of social learning in several taxa (reviewed by Galef, 2004; Reader & Biro, 2010; Whiten & Mesoudi, 2008). However, field experiments lack ecological validity: even if one can experimentally trigger a behaviour in wild animals, this does not automatically imply that animals rely on this behaviour during everyday life or that it is part of their natural behaviour.

Therefore, it remains unclear exactly for what and when individuals engage in social learning in the wild and observational studies on wild populations are needed to resolve this issue. Many species show social influences on foraging behaviour in the wild (Galef & Giraldeau, 2001; Rapaport & Brown, 2008). More specifically, several studies on wild primates and other mammals report a strong connection between the feeding behaviour of immatures and their mothers, including mountain gorillas, *G. g. beringei* (Watts, 1985), Japanese macaques, *Macaca fuscata* (Tarnaud & Yamagiwa, 2008), howler monkeys, *Alouatta palliata* (Whitehead, 1985), red-fronted lemurs, *Eulemur fulvus* (Tarnaud, 2004) and dolphins, *Tursiops* sp. (Mann & Sargeant, 2003). Matsuzawa et al. (2001) showed that chimpanzees rely on close observation of the mother and others when learning tool-supported nut cracking, a phenomenon they called 'master-apprenticeship'. This interpretation was confirmed by Lonsdorf, Eberly, and Pusey (2004), Lonsdorf (2006) and Humle, Snowdon, and Matsuzawa (2009). Similarly, wild chimpanzees and tufted capuchin monkeys, *Sapajus* spp., selectively seek out more skilled individuals to observe during tool-assisted foraging (Biro et al., 2003; Coelho et al., 2015; Ottoni, de Resende, & Izar, 2005). Work on capuchin monkeys, *Cebus capucinus* (Perry, 2009) and Bornean orang-utans, *Pongo pygmaeus wurmbii* (Jaeggi et al., 2010) found similar patterns for other complex foraging techniques.

These studies have shown that in various primates the acquisition of complex skills is socially influenced. However, highly complex skills such as tool use often seem to be superfluous for an individual's survival, since not all populations of a species show them. Few studies have examined whether primates also rely on social learning for the acquisition of the more basic routine skills. Social learning is contrasted with individual learning, which is often treated as the default option for any learning since animals are expected to rely on social information when they are unable to solve a problem independently (Laland, 2004). However, individual learning is time intensive and carries the risk of injury or poisoning. In contrast, social learning is more efficient and less risky. Social learning may therefore be more common than previously assumed, and might also be used for the acquisition of routine skills.

The aim of the present study was to examine the role of peering (attentive close range watching) in the skill acquisition process in immature orang-utans, including widespread and routine skills such as the processing of common food items or nest building. We did so by examining peering contexts, choice of experts and subsequent practice. We further aimed to validate peering as an index of an observational form of social learning in immature orang-utans. We used observational data collected during nest-to-nest follows of two populations of wild orang-utans, with special attention to indicators of social learning such as peering and different exploratory behaviours. Cross-sectional and longitudinal data composed of a body of more than 1500 peering events by 20 immature individuals allowed us to test detailed predictions about observation rates and contexts.

Orang-utans are an appropriate species for this kind of analysis. Wild orang-utans live in a complex foraging niche with a diet consisting of many difficult-to-process and hidden food items, many of which require tool use (van Noordwijk & van Schaik, 2005). Also, every evening they build a nest in which to spend the night. These nests are multilayered constructions in a tree or combination of trees and made of bent branches to which additional elements, such as pillows (small piles of small broken-off leafy twigs) or blankets (larger leafy twigs bent or laid over the nest, leaving the head area free), are added (Prasetyo et al., 2009). Before being weaned at the age of 6–9 years, infant orang-utans are in permanent association with their mother and share her nest (van Noordwijk, Sauren, Nuzuar, Morrogh-Bernard, Utami Atmoko, &

van Schaik, 2009). These mother–offspring associations are highly tolerant, including almost permanent body contact for the first 2 years, followed by a period of constant close distance (van Noordwijk et al., 2009). This should provide immature orang-utans with incentives and frequent opportunities for social learning, although in most populations adults lead a rather solitary life and rely on their own knowledge (Mitra Setia, Delgado, Atmoko, Singleton, & Van Schaik, 2009).

If immature orang-utans acquire their feeding and nest-building skills through peering, we can predict a variety of patterns in their peering behaviour. In this observational study we used a correlational approach to test the following predictions. (1) Peering is most likely to occur in contexts in which learning is possible, especially during feeding and nest building, rather than other contexts. (2a) Peering rates in the feeding context increase with increasing complexity and decrease with increasing frequency of the food item in the mother's diet. (2b) Peering in the feeding context is followed by increased rates of exploratory behaviours with the same food item, serving as practice. (2c) Peering rates in the feeding context decrease with age due to increasing feeding competence of the immatures. (3a) Peering in the nest-building context is followed by increased rates of nest practice behaviour. (3b) The age at which immatures show increased peering in the nest-building context coincides with the age at which they show increased nest practice behaviour. (3c) Peering rates decrease with increasing nest-building competence of the immatures. (4) As immatures grow older, peering directed at the mother gradually decreases because the mother's skills will have been acquired, whereas peering directed at other individuals increases, relative to total peering events.

METHODS

Data were collected from 2007 to 2015 on a population of wild Sumatran orang-utans, *Pongo abelii*, at the Suaq Balimbing research area (3°42'N, 97°26'E, Aceh Selatan, Indonesia) and a population of wild Bornean orang-utans, *P. p. wurmbii*, at the Tuanan research area (2°09'S, 114°44'E, Kalimantan Tengah, Indonesia). Both research areas consist mainly of peat swamp forest with relatively high orang-utan densities, with seven individuals per square kilometre at Suaq (Singleton, Knott, Morrogh-Bernard, Wich, & van Schaik, 2009) and four at Tuanan (van Schaik, Wich, Utami, & Odom, 2005). At both study sites behavioural observations had been ongoing for several years (starting in 1994 at Suaq and 2003 at Tuanan).

The research protocols were approved by the Ministry of research and technology (RISTEK; Research Permit No.: 152/SIP/FRP/SM/V/2012) and adhered to the legal requirements of Indonesia. As a strictly observational study on wild animals, we did not interact with our study animals in any way.

Data Collection

We collected 2571 h of behavioural data during full-day (nest-to-nest) focal follows. We followed an established protocol for orang-utan data collection (<http://www.aim.uzh.ch/de/research/orangutanetwork.html>), using focal animal sampling with instantaneous scan sampling at 2 min intervals as well as all-occurrence focal animal sampling of certain focal behaviours (see Table 1, Fig. 1). Data were collected by C.S. and other observers who all reached an index of concordance of more than 85% during interobserver reliability testing (based on simultaneous follows by multiple observers on the same focal animal without verbal

Table 1

Definitions of the focal behaviours used as measures of social learning, independent exploration and nest practice

Behaviour	Definition
Peering	Directly looking at the action of another individual sustained over at least 5 s, and at a close enough range that enables the peering individual to observe the details of the action (within 2 m in the feeding and within 5 m in the nest-building context). The peering individual is facing the demonstrator individual and shows signs of following the actions shown by the demonstrator by head movements
Exploration	Nonrepetitive, usually destructive manipulation of objects without apparent feeding purpose, as well as feeding attempts on a food item or any other object whereby the item is taken into the mouth but not properly ingested
Nest practice	Unsuccessful attempt to build a nest (by bending and intertwining leafy branches) or seemingly successful construction of a nest without using it



Figure 1. Dependent immature peering at its mother in the feeding context. Photo: Julia Kunz.

exchange about the activity of the focal animal). We defined the complexity of the food items by the number of steps it takes to process an item, as shown in Table 2. We assessed nest-building competence by the proportion of nights on which immatures built their own night nests: whereas young infants often build small, unstable nests during the day in which they take brief rests at most, orang-utans start building their own nest for night use only during late infancy or even after the onset of juvenility (van Noordwijk et al., 2009).

Data Sets

We collected data on 20 immatures (11 at Suaq and nine at Tuanan) over multiple years. To capture one specific developmental state of the immature animals, we pooled data collected on one individual within a period of 4 months to create a single age-specific individual mean. This resulted in 19 age/individual data points for Suaq and 12 age/individual data points for Tuanan (Appendix Table A1). Each age/individual data point consists of 50–110 h (mean = 83) of continuous observation. The age range and mean age of both data sets were comparable (Suaq: 0.5–12.3 years, mean = 5.21; Tuanan = 0.4–11.3 years, mean = 5.20). Here, we distinguish between three categories of immatures: (1)

Table 2
Processing steps of food items: descriptions of the most frequent steps and examples

Processing steps	Description	Example
0	Pick and eat	Leaves
1	(a) Pick, peel and eat; (b) Pick, eat and spit out	(a) Fruits with indigestible skin (b) Fruits with indigestible seed
2	(a) Pick, peel, eat and spit; (b) Pick, bite in half, extract inside, eat	(a) Fruits with indigestible skin and seed (b) Hard shell fruits with edible internal fruit flesh
3	(a) Pick, bite in half, scrape out inside, eat, spit out; (b) Collect, scratch or bite open, suck, eat	(a) Hard shell fruits with edible internal pulp and indigestible seed; (b) Insects embedded in wood or other substrate
4	(a) Break off, peel, extract inside, eat, spit out (b) Break off, examine, bite apart, suck, eat	(a) Vegetative material ('pith') inside branches and liana (b) Sucking insects out of dead twigs
5	Break off, peel (optional), chew (optional), insert into tree hole/ nest/ fruit, and then extract, collect insects/insect product/seeds from tool tip, eat, spit out (optional)	Tool use (tree hole, insect nests and fruits)

dependent immatures, who are between birth and weaning; (2) semi-independent immatures, who are weaned but still in permanent association with their mothers; and (3) independent immatures, who are no longer in permanent association with their mothers. Weaning age at Suaq is around 7–9 years and at Tuanan around 6–7.5 years (van Noordwijk & Schuppli, n.d.).

Data Analysis

All analyses and plots were done using R (R Development Core Team, 2011). Data were analysed using generalized linear mixed models (GLMM) using lmer as implemented in the package lme4 (Bates, Maechler, Bolker, & Walker, 2014). Individuals were included as a random factor to control for the fact that several individuals occurred multiple times in the data set. In one analysis there were no repeated measures, so we used a linear model (LM) as implemented in the package stats in R. Unless otherwise indicated, sample sizes for each model (N) represent the number of age-specific individual means (see above). Statistical significance of the fixed effects in the GLMMs was assessed using cftest of the multcomp package (Bretz, Hothorn, & Westfall, 2010). Simultaneous effects of different factors on peering rates were assessed by including them as fixed effects. Models and their factors were selected based on the Akaike information criterion. The best description of age effects was either linear or quadratic, depending on the response variable.

A total of 1536 peering events, mostly in the feeding and nest-building context could be included in the analysis. There were more peering events recorded at Suaq ($N = 1280$) than at Tuanan ($N = 256$) mostly because peering rates in the feeding context differed between sites. Thus, the more detailed analyses for the feeding context were only conducted with the Suaq data set. Even though definitions and data collection methods were the same across years and sites, data collection gradually became increasingly detailed. For instance, measurement of the timing of peering events and activities around the peering event were only available for data collected after 2010. Therefore, not all analyses include all data. Details on the statistical models and sample sized can be found in Appendix Table A2.

RESULTS

To investigate whether immature wild orang-utans rely on peering for the acquisition of their subsistence and social skills, we analysed all-occurrence data on peering and exploration gathered during nest-to-nest follows. We first excluded the possibility that peering served not to gather information, but instead to receive

food from the individual at whom the peering was directed. One could, however, reasonably argue that begging and receiving food may also facilitate learning (Jaeggi et al., 2008), and thus still qualify as social learning. We found that 15.6% of all food peering events were followed by food begging. Thus, begging cannot be responsible for any major patterns seen in peering. Moreover, in the following analyses, including or excluding begging did not alter the results. None the less, for the test of prediction 2b we excluded begging because after successful begging the immature obtains the item the mother is feeding on, and increased exploration rates with those items would thus not be conclusive in those cases.

Prediction 1

We found that at both sites most peering happened in the feeding context, followed by nest building. Less than 5.5% of peering events took place in a social context, such as mating, displaying at another individual, grooming or peering, or during other, nonsocial activities, including moving, resting, defecating and urinating or scratching (Fig. 2a). This finding is in line with the rarity of social interactions in orang-utans (Morrogh-Bernard et al. 2009).

When focusing on actual rates of peering (peering events of dependent immatures directed at the mother divided by the time the mother engaged in the peered-at activity), we found that activities in the social context as well as nest building were most frequently peered at, followed by feeding. Suaq immatures showed significantly higher peering rates than Tuanan immatures in the feeding context (GLMM, $N = 16$: Site (Tuanan): $b = -0.75$, $t = -3.51$, $P < 0.001$; Age: $b = 0.23$, $t = 2.20$, $P = 0.028$; Age²: $b = -0.03$, $t = -2.35$, $P = 0.019$; Fig. 2b), whereas there was no significant difference in the other contexts (Fig. 2b).

We analysed peering events in the feeding and nest-building context in more detail to test the predicted function of peering in social learning. For all other contexts, the number of peering events was too low for any detailed analysis.

Prediction 2a

We predicted peering rates would reflect the learner's state of ignorance, and thus increase with increasing processing complexity or increasing rarity of the food item. We examined peering of the Suaq dependent immatures at their mothers in the feeding context in relation to the number of steps needed to process the food item ('complexity'; Table 2) as well as the frequency of the food item in the mother's diet (in percentage of total diet, 'frequency'). To correct for the fact that food items are fed on for different amounts of

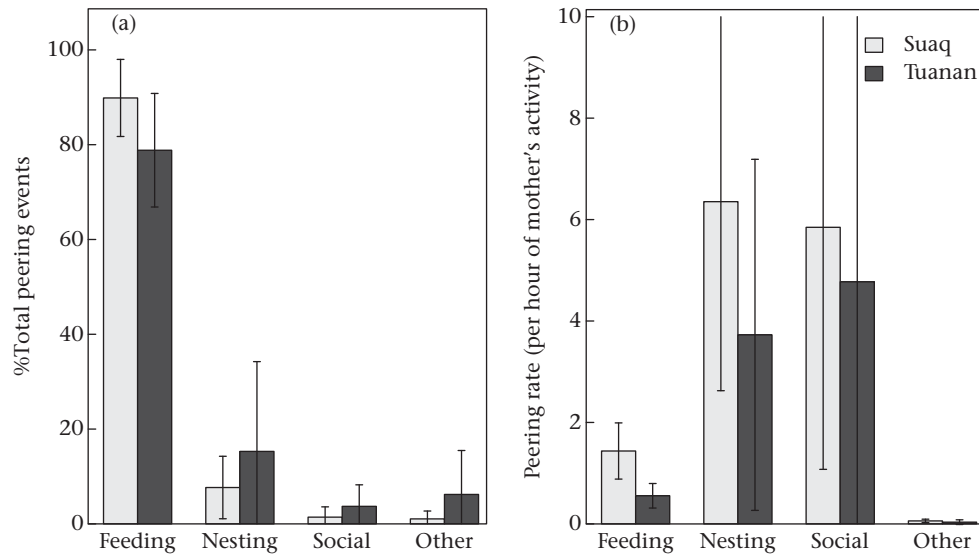


Figure 2. (a) Peering contexts: feeding, nesting, social interactions and others (all other, nonsocial activities), in percentage of total peering events for the different immatures at Suaq and Tuanan. (b) Peering rates: peering events at the mother per hour the mother spent doing the respective activity for the different dependent immatures at Suaq and Tuanan.

Table 3

GLMM with processing complexity of the food item ('complexity'), frequency of the food item in the mother's diet (log transformed; 'frequency') as well as age as fixed effects and individual as random effect

Effect	Type of effect	Estimate	<i>t</i>	<i>P</i>	<i>N</i> (180)	95% CI
Complexity	Fixed	0.10	5.89	<0.001	6	0.068 to 0.139
Log (frequency)	Fixed	−0.58	−17.12	<0.001	CV	−0.642 to −0.509
Age	Fixed	−0.04	−2.76	0.03	CV	−0.068 to −0.005
Individual	Random	—	—	—	9	—

The table shows estimates, *t* statistics, *P* values, number of levels for the categorical variables (*N*), where CV refers to continuous variables, and 95% confidence intervals (CI). The number in parentheses represents the total number of individual – food item combinations.

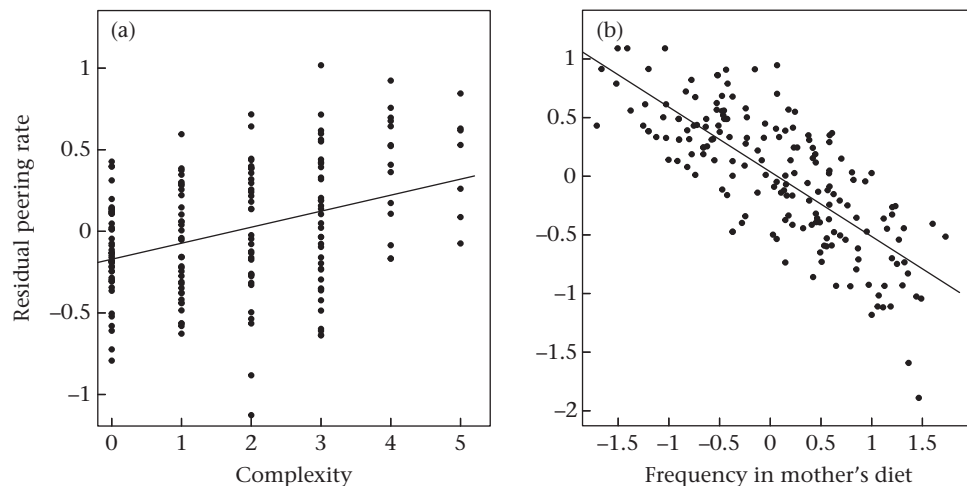


Figure 3. Peering in relation to food complexity and frequency in the mother's diet: (a) residual peering rates (corrected for frequency) versus complexity and (b) residual peering rates (corrected for complexity) versus frequency in the mother's diet (log transformed) for dependent Suaq immatures peering at their mothers in the feeding context. Residuals and the regression lines calculated based on them were used for illustrative purposes only.

time and therefore the offspring has varying opportunities to peer, we calculated peering rates by dividing the number of peering events recorded for a given food item by the time the mother was feeding on this item during mother–offspring associations. We

long-transformed the predictor variable 'frequency' and the response variable (peering rate) in order to reach randomly distributed model residuals. We found that dependent immatures peered significantly more frequently with increasing processing

complexity of the item and with decreasing frequency of the item in the mother's diet, whereas age had a significantly negative effect on peering rates (Table 3, Fig. 3a, b).

Prediction 2b

If immature orang-utans learn by observing others, peering should be followed by increased levels of exploratory behaviours or feeding attempts with the same food item, especially in unskilled foragers (dependent immatures). To investigate the effect of peering on exploratory behaviour, we determined the number of exploration events with the food item before and after each peering event when the immature was in the mother's feeding patch (see Appendix Fig. A1 for a more detailed description of how this was measured). Since peering often happens at the beginning of the mother's feeding bout, the dependent immature has naturally more time to explore after the peering bout, which might bias the results. Thus, to correct for varying opportunities for these behaviours to occur, we calculated peering rates by dividing the number of peering events by the time before or after the peering event, respectively. We only included peering events where the dependent immature was in the feeding patch for at least 2 min before and after the peering event.

We found that dependent immatures showed significantly higher rates of exploratory behaviour after peering than before peering (GLMM, $N = 14$: Timing: $b_g = 6.71$, $t = 4.83$, $P < 0.001$; Age: $b = 1.06$, $t = 2.76$, $P = 0.006$; Fig. 4).

To examine social influences on selective practice in more detail, we looked at stick exploration by immatures. Adult orang-utans habitually use sticks (broken-off twigs or dead sticks) only at Suaq, and do so in two feeding contexts: (1) as tools to extract insect products from tree holes as well as to get seed out of fruits (van

Schaik et al. 2003) and (2) to suck insects out of the ends of dead hollow twigs ('dead twig sucking'). Both feeding techniques involve 'mouthing' the end of the stick. We found a trend for dependent immatures at Suaq to explore sticks (using their mouth) more often than dependent immatures at Tuanan (GLMM, $N = 16$: Site (Tuanan): $b = -0.45$, $t = -1.93$, $P = 0.053$; Age: $b = 0.59$, $t = 2.64$, $P = 0.008$; Age²: $b = -0.09$, $t = -2.97$, $P = 0.003$; Fig. 5a). We also found that in the hour after peering at their mothers using a tool or performing dead twig sucking, dependent immatures at Suaq showed significantly increased rates of stick exploration (GLMM, $N = 10$: Context (after peering): $b = 0.78$, $t = 3.63$, $P < 0.001$; Age: $b = 1.3$, $t = 2.69$, $P = 0.007$; Age²: $b = -0.2$, $t = -3$, $P = 0.003$; Fig. 5a). Also, at Suaq dependent immatures manipulated the end of the stick in a higher percentage of all exploration events on sticks (LM, $N = 8$: Site: $b = -42.03$, $t = -4.2$, $P = 0.009$; Age: $b = 1.74$, $t = 0.61$, $P = 0.59$; Fig. 5b).

Prediction 2c

Under the assumption that peering is a means of social learning in the feeding context, we predicted that peering rates would reflect the learner's competence and should therefore decrease with increasing age and feeding competence. At both sites, peering rates in the feeding context initially increased, as immatures became more active and started to ingest more solid food, peaking around the age of 3 years and then decreasing. At the same time, their feeding rates (as a measure of feeding competence) increased. Overall peering rates (directed at adults as well as semi-independent and independent immatures) were significantly higher at Suaq than at Tuanan (GLMM, $N = 31$: Age²: $b = -0.01$, $t = -4.99$, $P < 0.001$; Site (Tuanan): $b = -0.64$, $t = -5.43$, $P < 0.001$; Fig. 6).

Prediction 3a

In the nest-building context we predicted that, as in the feeding context, peering would be followed by increased rates of practising nest building. Consistent with this we found that peering at another individual in the nest-building context led to significantly increased rates of nest practice behaviour in the peering individuals in the subsequent hour compared to the hour before the peering event (GLMM, $N = 20$: Timing: $b = 0.25$, $t = 4.76$, $P < 0.001$; Age: $b = 0.05$, $t = 1.45$, $P = 0.148$; Site (Tuanan): $b = -0.09$, $t = -0.61$, $P = 0.542$; Fig. 7a, b).

Predictions 3b, c

Under the assumption that nest peering serves for learning, the age at which immatures start to peer in the nest building context is expected to coincide with the age at which they start to practise nest-building behaviour. With increasing nest-building competence of the immature, nest practice behaviour is expected to decrease. Indeed, rates of nest peering were significantly correlated with rates of nest practice behaviour. Both nest peering rates and nest practice rates followed the same age trajectory (Fig. 8). We also found that with increasing age and proportion of own night nest-building attempts nest peering rates decreased (Fig. 8). There was no significant difference in nest peering rates between the study sites (GLMM (Nestpeering ~ NestPractice + Site + (1|Individual)), $N = 14$: Nest practice: $b = 0.42$, $t = 5.56$, $P < 0.001$; Site (Tuanan): $b = 0.003$, $t = 0.2$, $P = 0.839$).

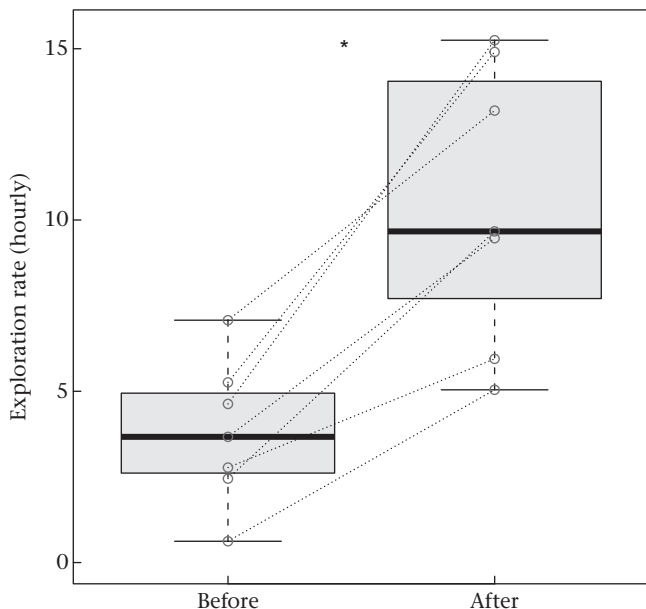


Figure 4. Peering and selective exploration: average hourly rates of exploratory behaviour with the same food item before and after peering events at the mother, when the immature was within the same feeding patch for dependent immatures at Suaq. The data points represent exploration rates of the different infants before and after the peering event, averaged over all their recorded food peering events. The circles represent individual average exploration rates of each context. The dotted lines connect exploration rates of the same individual. The horizontal line indicates the median, the box the upper and lower quartile, and the whiskers the greatest and lowest value, respectively. * $P < 0.05$.

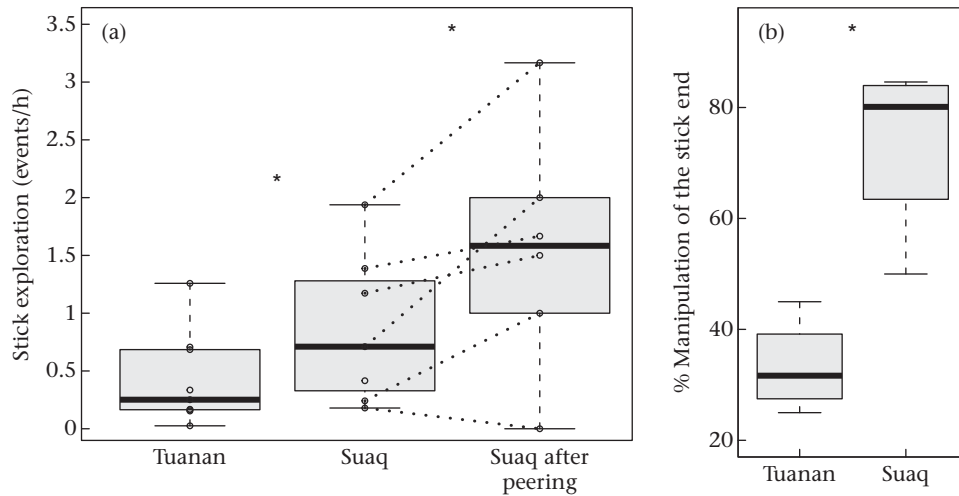


Figure 5. Stick use practice. (a) Average hourly rates of exploration events on sticks (using their mouth) for dependent immatures at Tuanan and Suaq over all observation hours, as well as for the Suaq dependent immatures in the hour after they had been peering at the mother using a stick tool or sucking dead twigs. The circles represent individual stick exploration rates. The dotted lines connect individual averages for each state. (b) Average percentage of exploration events on sticks that were focused on the end of the stick (as opposed to any other part of the stick) for the infants at Suaq and Tuanan. The horizontal line indicates the median, the box the upper and lower quartile, and the whiskers the greatest and lowest value, respectively. * $P < 0.05$.

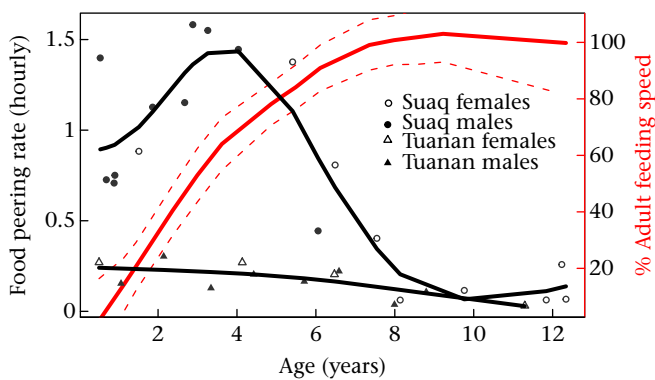


Figure 6. Peering in relation to age and feeding competence: hourly peering rates in the feeding context (at adults as well as semi-independent and independent immatures) versus age (in years). The black solid lines summarize the course of food peering rates versus age for each population, using smoothing functions (smooth spline function of the stats package in R). The red (rising) line shows average feeding rate as a percentage of average adult female feeding speed, with 95% confidence interval, again using a smoothing function (based on Schuppli, Zweifel et al., n.d.).

Prediction 4

If peering is a means of social learning, with increasing age immatures should peer more frequently at other individuals with potentially new techniques compared to their (familiar) mothers. To test this, we compared dependent immatures' peering rates at their mothers with those at other adult and independent immature individuals. Because younger dependent immatures rely on their mothers for transport, and thus show a strong bias in association, we had to control for the number of opportunities by including cases where the dependent immature was within 2 m of a role model. We therefore calculated the relative proportion of peering directed at the mother versus other role models corrected for the time they spent within 2 m of each class of role model. We only included individuals that had spent at least 60 min within 2 m of each type of role model over the total follow period to control for lack of opportunities. As predicted, we found that with increasing age, the proportion of peering directed at the mother decreased. From the age of 3–4 years, when they were fully capable of

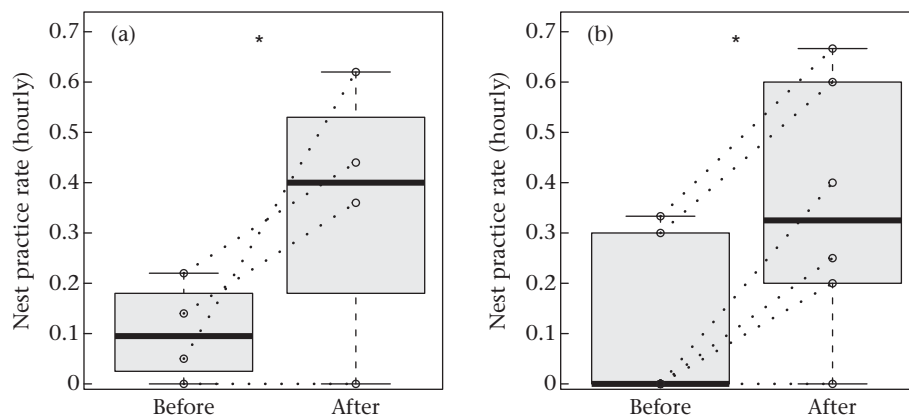


Figure 7. Nest peering and nest practice behaviour: average hourly rates of nest practice behaviour 1 h before and after nest peering of dependent immatures at (a) Suaq and (b) Tuanan. The circles represent individual nest practice rates before and after the peering event, averaged over all nest peering events. The dotted lines connect individual averages for each state. The horizontal line indicates the median, the box the upper and lower quartile, and the whiskers the greatest and lowest value, respectively. * $P < 0.05$.

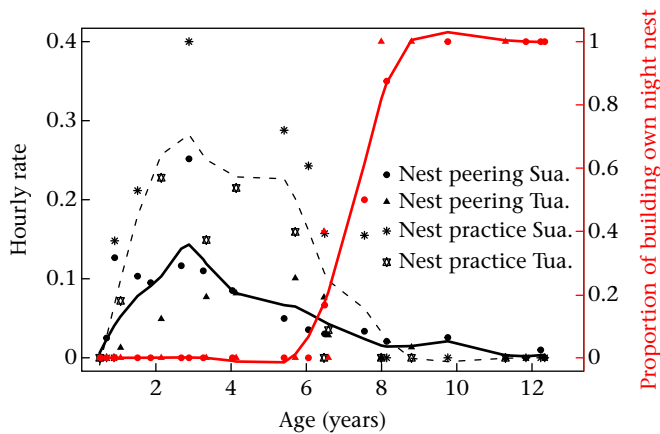


Figure 8. Nest peering and nest practice behaviour in relation to age and nest-building competence: rates of nest peering and nest practice and the proportion of nights on which immatures built their own nest (although they did not necessarily spend the entire night in it) as a function of age for the Suaq immatures. The dashed line represents the course of nest practice rates over age, the solid line the course of nest peering over age and the red line the course of proportions of night an own night nest was built over age, using smoothing functions. We obtained all smoothing functions via the smooth spline function of the stats package in R.

independent locomotion, dependent immatures preferred other individuals over the mother as peering targets. These other individuals were mainly adult males (which were probably unrelated), followed by semi-independent and independent immatures (siblings, as well as unrelated immatures) and other mothers (mostly related ones). There was no difference in the relative proportions of peering directed at the mother versus other individuals between the sites (GLMM, $N = 36$: Age: $b = -0.08$, $t = -4.18$, $P < 0.001$; Site: $b = -0.02$, $t = -0.26$, $P = 0.794$; Fig. 9).

DISCUSSION

The aim of this study was to test the prediction that immature orang-utans, under natural conditions learn their skills by observing conspecifics. To do so we looked at the rates and the

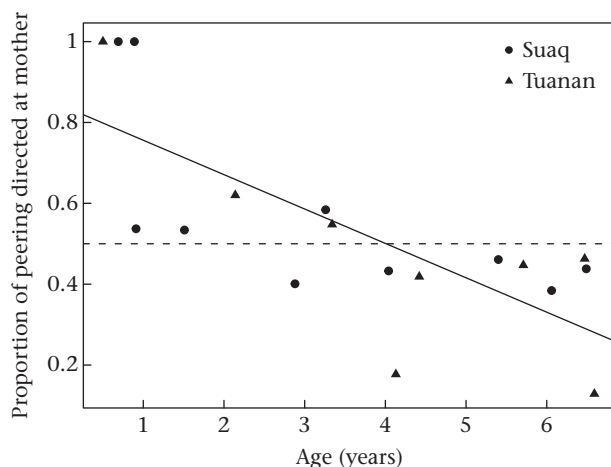


Figure 9. Peering at mother versus peering at others: proportion of peering directed at the mother (versus other individuals) versus age for dependent immatures at Suaq and Tuanan. A value of 0.5 indicates an equal proportion of peering directed at the mother and other individuals.

context of peering and exploratory behaviour in immatures from two populations. It could be argued that the desire to acquire information is not the sole underlying motivation of orang-utan peering behaviour. However, if information is transferred through peering, irrespective of the original motivation of the peering individual, we expect peering behaviour to meet a variety of predictions, which we tested in this study.

We found that peering was most frequent in contexts in which learning was expected and that peering decreased with increasing competence. The peering data show why it takes immature orang-utans several years to acquire their feeding skills and more complex feeding skills such as tool use take longest to develop (Meulman, 2014, van Noordwijk & van Schaik, 2005, Schuppli, Zweifel, Forss, van Noordwijk, M. A. & van Schaik, n.d.). Similarly, nest building seems to be acquired over several years and nest quality only gradually increases (Russon, Handayani, Kuncoro, & Ferisa, 2007; van Noordwijk & van Schaik, 2005; van Noordwijk et al., 2009). Thus, rather than being developmentally canalized or imprinted, feeding and nest building are acquired through a learning process, using both social inputs and individual practice. By the age of 12 or 10 years, Sumatran and Bornean orang-utan immatures, respectively, have reached adult-like diet repertoires and feeding rates (Schuppli, Zweifel et al., n.d.). By that time, peering rates in the feeding and nest-building context have strongly declined. However, some peering continues beyond that age, especially when individuals meet unfamiliar associates, which is consistent with the results of experiments on chimpanzee nut cracking (Inoue-Nakamura & Matsuzawa, 1997).

We found that peering rates in the feeding context were lower for the more familiar food items in the mother's diet, consistent with findings on Japanese macaques (Tarnaud & Yamagiwa, 2008). This pattern is consistent with several social learning mechanisms, including simple ones, such as stimulus enhancement. As a purely observational study it is difficult to pin down the learning mechanism at work. However, because peering rates were significantly higher for food items with greater processing complexity, the use of observational learning is the most plausible, especially given the fact that captive and rehabilitant orang-utans are capable of observational learning (Dindo et al., 2011; Russon & Galdikas, 1993; Stoinski & Whiten, 2003). We further found significant differences in peering rates and contexts between the study sites (Schuppli, Forss, Meulman, van Noordwijk, M. A. & van Schaik, n.d.).

If peering is a means of social learning, rates of selective practice should increase following peering, especially for unskilled individuals (younger dependent immatures). Our results confirmed this. First, in the nest-building context, peering coincided with the onset of nest-building practice. Furthermore, nest peering led to significantly increased rates of nest practice in the hour after peering. During nest practice immatures show the same types of manipulation of leafy branches as adults do when building their nests. Immature orang-utans are surrounded by leafy branches all day long. However, the fact that they only start manipulating these in ways adults do when building nests after observing their mothers doing so, hints towards an observational form of social learning. Second, dependent immatures' rates of exploratory behaviours with the same food item significantly increased after peering: Within the same feeding bout of the mother and when already the immature was within the same feeding patch, exploration rates were significantly lower before the peering event than after the peering event. Thus, even though the immatures were already in close proximity to the food items and their mothers, their exploration rates only increased after they had observed their mother feeding on these items. Finally, we found more practice-like

stick manipulations at Suaq, the site where adults habitually use sticks in the feeding context, namely during tool use and dead twig sucking. Stick exploration rates increased most after the immatures had been peering at their mothers using tools or dead twig sucking. In fact, immatures at Suaq were more likely to manipulate sticks at the end part, just as adults do during tool use and dead twig sucking. These patterns strongly suggest that the observed effects were due not to local enhancement or social facilitation but to observational learning.

The fact that exploration increased after peering also suggests that exploration is partly triggered by attention paid to role models. This is consistent with findings in gorillas (Watts, 1985) and howler monkeys (Whitehead, 1985), where immature feeding and exploration behaviour is linked to the feeding bouts of their mothers. However, no such link was found in Mayotte brown lemurs, *E. fulvus* (Tarnaud, 2004), where juveniles explore food items regardless of their mothers feeding activity.

In conclusion, orang-utans, and presumably some, but not all other primate species, learn their foraging and nest-building skills through close observation of these actions by experts. Immature orang-utans also show targeted practice of the same actions after observing expert individuals performing these actions. This is consistent with Galef's (2015) suggestion that template matching, through an interplay of social and asocial learning, helps the learning individual to iteratively produce a match between its performance and the observed actions of a demonstrator, which has recently been confirmed in chimpanzees (Whiten, 2015).

We anticipated that older immatures who had already acquired most of their mother's skills would show increasing interest in role models other than the mother. Our results supported this prediction: whereas young dependent immatures exclusively peered at their mothers, they increasingly peered at others as they got older. By the age of weaning, immatures showed a clear preference for these less familiar role models. Our results are also consistent with the notion that with increasing age, immatures are less reliant on the mother and thus, in general, show more interest in other individuals, irrespective of the skills of these individuals. However, the fact remains that immatures did indeed peer at these individuals. Wild chimpanzees (Inoue-Nakamura & Matsuzawa, 1997) and Siberian jays, *Perisoreus infaustus* (Griesser & Suzuki, 2016) show a similar pattern under experimental conditions. These findings are also consistent with the phenomenon of social referencing in human infants, who are exclusively oriented towards familiar caregivers in the first few years of life and only gradually extend their interest and trust towards less familiar individuals (e.g. Feinman, 1982).

Our study suggests that under natural conditions immature orang-utans learn by observing others and rely heavily on social learning for skill acquisition. In this species, and perhaps others that need to learn many skills and have intergenerational associations, social learning might be the default mode of learning. This is in line with laboratory experiments that have shown that socially deprived animals have severe deficits in a broad range of skills (Brent, Bloomsmith, & Fisher, 1995; Harlow, Dodsworth, & Harlow, 1965; Mason, 1968; Schrijver, Pallier, Brown, & Wurbel, 2004). Our results are also consistent with the earlier finding that in orang-utans, diet must be socially learned since offspring inherit the diet repertoires of their mothers (Jaeggi et al., 2010). This study also provides further evidence that observational learning is the mechanism that underlies the variation in feeding and nest-building techniques between different orang-utan populations (Bastian, Zweifel, Vogel, Wich, & van Schaik, 2010; Krutzen et al., 2011).

Humans rely heavily on social learning, and do so with uniquely high fidelity (Horner & Whiten, 2005; McGuigan, Whiten, Flynn, & Horner, 2007). Social learning allows for the accumulation and transfer of knowledge over successive generations (van Schaik & Burkart, 2011). During human evolution, the ability to learn from others enabled our ancestors to occupy a greater variety of habitats than any other mammal species. Strikingly, no individual human being would be able to individually acquire the skills necessary to survive in any of these habitats (Boyd, Richerson, & Henrich, 2011). It has therefore been argued that the difference in cognitive abilities between us and our closest relatives, the great apes, in itself is not enough to explain the difference in species' success, but that the key must lie in the extent of social transmission (Boyd et al., 2011). Since we showed that orang-utans rely heavily on observational learning under natural conditions, this alone cannot be the cause of the massive difference between humans and great apes. Instead, there are two other likely causes. First, compared to great apes, humans show a much larger network of tolerant experts (van Schaik & Pradhan, 2003). Second, humans systematically rely on imitation and teaching whereas great apes do not (Tomasello, 1994). However, given the role of practice (Galef, 2015), imitation may not be as critical as previously assumed. Teaching, however, is pronounced in humans (Kline, 2015), and may also be linked to the adoption of extensive allomaternal care by our ancestors (Burkart, Hrdy, & Van Schaik, 2009).

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Appendix

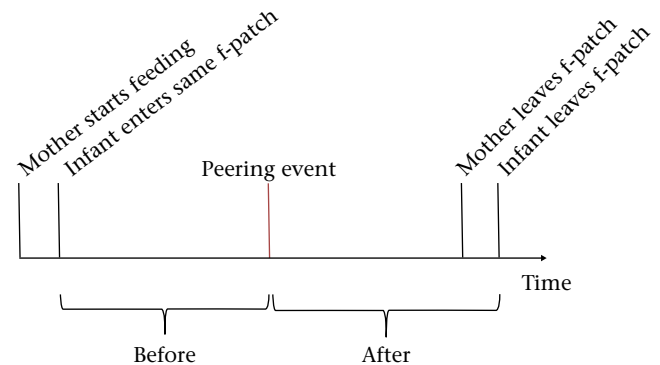


Figure A1. Explanation for the analysis of Fig. 4: to see whether exploration rates increase after a peering event, for each dependent immature we calculated average hourly rates of exploratory behaviour with the same food item before and after peering events. We only included peering events directed at the mother. For each peering event we looked at the immatures' exploration rates for the time they were within the same feeding patch ('f-patch') as the mother. 'Before' refers to the amount of time before the peering event, 'after' to the time after the peering event.

Table A1

Study site, name of the focal animal, age and sex class, observation period and age for the 31 age individual data points

N	Site	Focal	Age class	Sex	Observation	Age
1	Suaq	Lois	Dependent	M	2011	0.5
2	Suaq	Rendang	Dependent	M	2014	0.7
3	Suaq	Simba	Dependent	M	2013/14	0.9
4	Suaq	Frankie	Dependent	M	2013	0.9
5	Suaq	Cinnamon	Dependent	F	2013	1.5
6	Suaq	Ronaldo	Dependent	M	2007/08	1.9
7	Suaq	Fredy	Dependent	M	2007	2.7
8	Suaq	Lois	Dependent	M	2013	2.9
9	Suaq	Fredy	Dependent	M	2008	3.3
10	Suaq	Fredy	Dependent	M	2009	4.0
11	Suaq	Chindy	Dependent	F	2008	5.4
12	Suaq	Fredy	Dependent	M	2010/11	6.1
13	Suaq	Lilly	Dependent	F	2007/08	6.5
14	Suaq	Lilly	Dependent	F	2008/09	7.5
16	Suaq	Chindy	Independent	F	2010/11	8.1
15	Suaq	Lilly	Independent	F	2011	9.8
18	Suaq	Ellie	Independent	F	2010/11	11.8
17	Suaq	Shera	Independent	F	2010/11	12.2
19	Suaq	Lilly	Independent	F	2014	12.3
20	Tuanan	Kahiyu	Dependent	F	2012	0.4
21	Tuanan	Joya	Dependent	M	2012	1.0
22	Tuanan	Danum	Dependent	M	2012	2.1
23	Tuanan	Joya	Dependent	M	2014	3.3
24	Tuanan	Mawas	Dependent	F	2012	4.1
25	Tuanan	Petzy	Dependent	F	2012	4.4
26	Tuanan	Kino	Dependent	M	2012	5.7
27	Tuanan	Mawas	1/2 dependent	F	2014/15	6.5
28	Tuanan	Jip	Dependent	M	2012	6.6
29	Tuanan	Deri	Independent	M	2012	8.0
30	Tuanan	Jip	Independent	M	2014	8.8
31	Tuanan	Milo	Independent	F	2012	11.3

M: male; F: female.

Table A2

Details on the statistical analyses for each prediction

Prediction	Model	Dependent variable	Effect	Type of effect	Estimate	<i>t</i> statistic	<i>P</i> value	<i>N</i>	95% CI
1	GLMM	Food peering rate (dependent immatures at Suaq and Tuanan)	Age	Fixed	0.23	2.2	0.028	CV	0.195 to 0.422
			Age ²	Fixed	0.03	−2.35	0.019	CV	−0.034 to −0.026
			Site (Tuanan)	Fixed	−0.75	−3.51	<0.001	2	−0.762 to −0.672
			Individual	Random	—	—	—	12 (15)	—
2b	GLMM	Exploration rate (dependent immatures at Suaq)	Timing (after peering)	Fixed	6.71	4.83	<0.001	2	4.103 to 9.32
			Age	Fixed	1.06	2.76	0.006	CV	0.343 to 1.761
			Individual	Random	—	—	—	6 (14)	—
									—
2b (stick)	GLMM	Stick exploration rate (dependent immatures at Suaq and Tuanan)	Age	Fixed	0.59	2.64	0.008	CV	0.187 to 0.991
			Age ²	Fixed	−0.09	−2.97	0.003	CV	−0.148 to −0.036
			Site (Tuanan)	Fixed	−0.45	−1.93	0.053	2	−0.878 to −0.03
			Individual	Random	—	—	—	13 (16)	—
	GLMM	Stick exploration rate (dependent immatures at Suaq)	Timing (after peering)	Fixed	0.78	3.63	<0.001	2	0.339 to 1.215
			Age	Fixed	1.3	2.69	0.007	CV	0.687 to 1.917
			Age ²	Fixed	−0.2	−3	0.003	CV	−0.291 to −0.118
			Individual	Random	—	—	—	5 (10)	—
	LM (<i>N</i> =5 (10))	End manipulations in percentage of total stick manipulations (dependent immatures at Suaq and Tuanan)	Age	Fixed	−42.03	0.61	0.568	CV	−67.79 to −16.27
			Site (Tuanan)	Fixed	1.74	−4.2	0.009	2	−5.58 to 9.05
3a	GLMM	Nest practice rate (dependent immatures at Suaq and Tuanan)	Timing (after peering)	Fixed	0.25	4.76	<0.001	2	0.146 to 0.355
			Age	Fixed	0.05	1.45	0.542	CV	0.049 to 0.071
			Site (Tuanan)	Fixed	−0.09	−0.61	0.148	2	−0.106 to −0.036
			Individual	Random	—	—	—	9 (20)	—
3b+c	GLMM	Nest peering rate (immatures at Suaq and Tuanan)	Nest practice rate	Fixed	0.42	5.56	<0.001	CV	0.279 to 0.572
			Site (Tuanan)	Fixed	0.003	0.2	0.839	2	−0.026 to 0.032
			Individual	Random	—	—	—	18 (26)	—
4	GLMM	Proportion of peering directed at mother (immatures at Suaq and Tuanan)	Age	Fixed	−0.08	−4.18	<0.001	CV	−0.122 to −0.046
			Site (Tuanan)	Fixed	−0.02	−0.26	0.794	2	−0.184 to 0.139
			Individual	Random	—	—	—	18 (36)	—

The table shows model type, dependent variable (with the sample described in parentheses), effects, type of effects, estimates, *t* statistics, *P* values (with significance at the 5% level indicated in bold font), *N* (where the number in parentheses next to the *N* individual is the total number of individual – age – timing combinations for each model and CV refers to continuous variables), and 95% confidence intervals, (CI).