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ORIGINAL ARTICLE

Effect of repeated exposures and sociality on novel food acceptance and consumption by orangutans

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Abstract Hundreds of rehabilitant great apes have been released into the wild, and thousands await release. However, survival rates after release can be as low as 20 %. Several factors influence individuals' survival rates, one of which is the capacity to obtain an adequate diet once released. Released individuals are faced with a mixture of familiar and novel foods in an unfamiliar forest; therefore, it is important to understand how they increase acceptance and consumption of novel foods. This is especially vital for omnivorous species, such as wild great apes, which consume several hundred species of different foods. We assessed the effects of repeated exposures and sociality (i.e. co-feeding in the presence of one or more other individuals) on the acceptance and consumption of novel foods by captive orangutans (*Pongo* sp). Repeated exposures of food (novel, at first) did not cause an increase of acceptance of food; in other words, the orangutans did not start to eat a food item after being exposed to that food more often, but repeated exposures of food increased consumption (i.e. quantity). After repeated exposures, the orangutans also became gradually more familiar with the food, decreasing their explorative behaviour. The presence of co-feeding conspecifics resulted in an increased acceptance of the novel food by orangutans, and they ate a larger amount of said foods than when alone. Repeated exposure and sociality may benefit rehabilitant great apes in augmenting and diversifying diet and, once practiced before release, may accelerate an individuals' adaptation to their new habitat, improving survival chances. Great ape rescue, rehabilitation and reintroduction require large financial and logistic investments; however, their effectiveness may be improved at low cost and low effort through the suggested measures.

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Introduction

All great ape species in the wild are either endangered or critically endangered (IUCN 2013). Preventive conservation measures such as habitat protection, guidelines for reduced-impact logging (Morgan and Sanz 2007; OCSP 2010; Hardus et al. 2012), and awareness and law enforcement campaigns (Wrangham and Ross 2008; Meijaard et al. 2011a; Meijaard et al. 2011b) are being implemented with varying degrees of success. At the same time, an important corrective conservation measure is rehabilitation/reintroduction. Rehabilitation of great apes commenced in the 1960s with the vision of restoring the populations of these endangered species (Beck et al. 2007). However, available data yield survival rates of reintroduced great apes between 20 and 86 %, with few data published about the effects of introduction on population growth and persistence of such populations (Russon 2009; Russon et al. 2009).

Successfully adjusting to forest life depends on a number of behavioural adaptations that are related to diet choices, nesting, locomotion and anti-predator responses (Rijksen 1978). In omnivore species, such as great apes, a varied and nutritional diet increases the chances of survival and constitutes the energetic basis for all other behaviours. Thus, knowledge about which food items can be eaten and those that should be avoided is crucial for survival. In golden lion tamarins (*Leontopithecus rosalia*), for example, consumption of toxic fruits and starvation caused the death of nearly 20 % of reintroduced animals (Beck et al. 1991). Great apes are known to have a diverse diet, with each consuming several hundred different species (Rodman 2002; Russon 2009; Russon et al. 2009). For instance, at one particular long-term research site (Ketambe, Sumatra), wild Sumatran orangutans (*Pongo abelii*) have been observed to eat 512 plant items (e.g. fruits, leaves, flowers) from a total of 379 plant species (Russon 2009; Russon et al. 2009). In a comparison between reintroduced and wild orangutans, the diet of the former approached that of the latter 2 years after resuming forest life (Russon 2009; Russon et al. 2009): however, an inadequate diet remained one of the common causes of death for reintroduced orangutans (Russon 2009; Russon et al. 2009). Furthermore, reintroduced orangutans are known to often consume unusual food items, ignore important food sources that are consumed by their wild counterparts and in general maintain a relatively narrow diet, all of which are factors that may jeopardise their long-term survival (Russon 2002; Grundmann 2006; Russon 2009; Russon et al. 2009). Ignorance of important food sources is likely the result of the lack of social food knowledge learned from the mother and/or peers, with reintroduced orangutans having to rely more on trial and error regarding the suitability of novel foods. Such exploratory behaviour in wild orangutans is, however, regarded as trivial as studies have shown that they rely primarily on tutors or models for learning about new foods (Bastian et al. 2010; Jaeggi et al. 2010). Therefore, to understand how reintroduced populations could better increase their diets both qualitatively and quantitatively would be beneficial to such projects and serve to increase success rates.

Table 1 Percentage of specific novel foods that are accepted, tried, and rejected and refused by the orangutans at the start of experiment 1 (repeated exposures)

Location	Food item	Accepted	Tried and rejected	Refused
GATI	Tortellini, green	0.42	0.08	0
GATI	Kidney beans	0.00	0.42	0
GATI	Date	0.50	0.00	0
GATI	Basil	0.08	0.50	0
AZ	Japanese leaf	0.24	0.29	0.25
AZ	Mozarella	0.29	0.14	0.25
AZ	Olive	0.24	0.29	0.25
AZ	Tortellini, green	0.24	0.29	0.25
BQC	Cheese	0.25	0.1	0.25
BQC	Spinach	0	0.3	0.75
BQC	Lime	0.25	0.3	0
BQC	Olive, black	0.5	0.3	0

There are several factors influencing the degree of caution towards novel food (referred to as *neophobia*) in primates, such as type of food (Visalberghi and Fragaszy 1995; Visalberghi et al. 2002; Visalberghi et al. 2003), number of exposures (Birch and Marlin 1982; Visalberghi et al. 1998; Wardle et al. 2003), post-ingestion consequences (Matsuzawa and Hasegawa 1983) and social influences (Cambefort 1981; Visalberghi et al. 1998; Johnson 2000; Yamamoto and Lopes 2004; Addessi et al. 2005; Addessi and Visalberghi 2006). In this study, we test the impact of the number of exposures and social influences on the acceptance and consumption of novel food items in captive orangutans.

We first hypothesise that if orangutans are exposed numerous times to the same palatable food (novel, at first instance), they will accept and/or consume that food item more often than after one or more exposures as a result of familiarisation with said item. This has been the case with humans and other nonhuman primates (e.g. Birch 1979; Birch and Marlin 1982; Addessi et al. 2004). We use novel food acceptance by orangutans in an experimental setting to assess the probability of novel sampling in a wild setting upon repeatedly encountering such novel food (e.g. synchronous fruiting of trees of the same species throughout the forest).

Our second hypothesis is that if orangutans are in a group rather than alone, their acceptance and consumption of novel food will increase when other members are feeding on the same item at close range. Wild orangutans live in dispersed fission-fusion communities and occasionally come together into (passive and active) foraging parties of several individuals, which can last for several days (Delgado and van Schaik 2000; Mitra Setia et al. 2009). Such feeding tolerance may increase the level of acceptance of novel food (e.g. Birch 1980; Addessi et al. 2004).

Methods

Subjects

Experiments were conducted with captive orangutans at three locations: Batu Mbelin Quarantine Center (BQC: Sumatra, Indonesia), Apenheul Zoo (AZ: The Netherlands) and Great Ape Trust of Iowa (GATI: US) between January 2009 and February 2010 (Supplementary Tables 1, 2). At each location, only individuals who could be separated were involved in the experiments (9, 7 and 6 individuals, respectively), irrespective of whether they were normally housed alone or with conspecifics. All were tested on a voluntary basis. The experiments complied with current Indonesian, Dutch and US laws.

General procedure

Food items used in the experiments were discussed with animal caretakers prior to the experiments to assess which were likely part of their dietary record. The individuals were not deprived of food before and the timing did not interfere with regular feeding times. Pilot trials were conducted to familiarise observers (one person video recording and one recording behavioural data), caretakers (i.e. presenting food items) and the orangutans with the procedure. Pilot trials were not considered for analyses. All experiments were recorded with a Sony HDV 1080i (at BQC), a Canon FS100 video-recorder (at GATI) and a Panasonic DMC-T25 digital camera (at AZ). The order of the individuals who participated was pseudo-randomised (i.e. according to the individual's eagerness to participate at each session).

During the experiments the orangutans could not see food items other then the item being tested. Operational definitions are as follows: an individual was considered finished with a food item when chewing ceased or no further attention was given to it for more than 30 s. Acceptance was defined as an individual picking up a food item and consuming it. Trial with subsequent rejection was considered to be when an individual picked up an item, started eating, but quickly dropped it before further ingesting any part. Refusal was considered to be picking up and immediately dropping the item without eating any part or a lack of picking up the item. Statistical analyses were conducted using IBM SPSS 19 (2010, SPSS, Inc.).

Experiment 1: repeated exposure of novel food

The effect of repeated exposure on the acceptance of novel food and consumption was investigated in 21 orangutans (Supplementary Table 1). Four different items, initially novel, were presented to the individuals. This procedure was repeated for 8 consecutive days using the same food items (Supplementary Table 2). Each item was presented separately, and the next was only presented when the subject consumed or refused the previous one. Level of acceptance across time was scored as refusal (1), trial with subsequent rejection (2) or acceptance (3) of the food item. These three mutually exclusive categories were averaged per individual per session for the purpose of analyses. Food items were weighed directly before and after to calculate the amount eaten by the individual. To quantify exploratory behaviour, the observer recorded individual instances of smelling or looking down at a food item in its mouth by protruding her lower lip (Table 1).

Mixed model analyses were conducted to examine the effect of repeated exposure on each of the four measures, viz. acceptance or refusal, amount of food eaten, number of looks and number of smells. In each, day was included as a fixed effect variable, while the intercept and slope of the respective measure for each individual were included as random effects. This allowed for controlling intra-individual differences (thus including differences in gender, age and birth place) in the magnitude of each measure and its increase or decrease across the 8 days. Possible covariance between intercepts and slopes across individuals was controlled for as well.

Experiment 2: social influences on novel food acceptance and consumption

The effect of social influences on the acceptance and consumption of novel food was investigated in 11 orangutans (Supplementary Table 1). This smaller sample size was mostly due to the quarantine status of individuals at BQC resulting in the inability to group them. Across 2 days, six novel food items (Supplementary Table 2) were presented, with on day 1 individuals on their own and on day 2 together in a group (≥2 individuals). All individuals were thus acquainted with each item when it was presented to the group. Food items were set in front of the orangutan enclosure and, when orangutans were in a group, items were arranged in such way that food was accessible to all orangutans in the group. The six novel food items were presented separately and in sequence, with each presented after all had consumed or refused the previous item. Level of acceptance and amount consumed were measured as described in experiment 1. Explorative behaviour, as measured by the number of looks and smells, could not be measured. General linear model analyses were carried out to examine the effect of sociality on acceptance and amount of novel food consumed when alone and when in a group as repeated measures.

Results

Experiment 1: repeated exposures

After the first day the percentage of acceptance of novel food items was 46.7 %, the percentage of trial with rejection was 42.4 %, and the percentage of refusal was 10.9 %. Repeated food exposure did not have a significant effect on the level of acceptance [mixed model analysis: $b = -0.02$, $t(21.3) = -1.49$, $P = 0.15$], that is, after 8 consecutive days no increase in the acceptance rate of the food by the orangutans was found. However, repeated food exposure had a significantly positive linear effect on the amount consumed [mixed model analysis: $b = 2.98$, $t(21.9) = 3.66$, $P = 0.001$]. We also checked for a possible quadratic or cubic effect, but these were not found ($P > 0.7$). That is, the amount of food eaten did not increase in proportion to the square or the cubic of the amount of days. Repeated exposure had a significantly negative linear effect on the number of looks [mixed model analysis: $b = -1.09$, $t(109.9) = -4.82$, $P < 0.001$] and a small but significant positive quadratic effect [$b = 0.057$, $t(152) = 2.92$, $P = 0.004$], which means that the number of looks decreased intensively per subsequent day. Finally, repeated exposure had a significantly negative linear effect on the number of smells [mixed model analysis: $b = -0.80$, $t(157.9) = -3.75$, $P < 0.001$] as well as a positive quadratic effect [$b = 0.14$, $t(152) = 2.66$, $P = 0.009$] and a negligible cubic effect [$b = -0.008$, $t(152) = -2.18$, $P = 0.03$]. Location did not affect the results. Because the subjects were nested within location, such effects were accounted for by individual variation in intercepts and slopes. This was verified by repeating the analyses, using individual × location as subject, which yielded the same result values.

In summary, repeated exposures did not affect the frequency with which orangutans chose novel foods; however, across repeated exposures orangutans increased the amount of food intake and became familiar with the food, displayed as a decreasing amount of explorative behaviours towards it, as measured by the number of looks and smells (Fig. 1).

Experiment 2: social influences

Sociality had a significant effect on the acceptance of food item (Greenhouse-Geisser test: $F = 23.170$, $P < 0.001$) with a significant linear contrast ($F = 23.170$, $P < 0.001$) as well as on the amount of food consumed (Greenhouse-Geisser test: $F = 19.125$, $P < 0.001$), also with a significant linear contrast ($F = 19.125$, $P < 0.001$). Thus, they accepted the novel items more and ate a larger amount when in a group than when alone (Fig. 2).

Discussion

Repeated exposures to food items had a positive effect on the consumption of food: captive orangutans quantitatively ate more of a food (novel, at first) when exposed more frequently to it. At the same time, orangutans became more familiar with the previously novel foods, as seen from the decrease in explorative behaviour towards them. To our knowledge, the effect of repeated exposures of novel foods has only been studied in one other nonhuman primate, the capuchin monkey (*Cebus apella*), with the study showing similar results, i.e. an increase in consumption and decrease

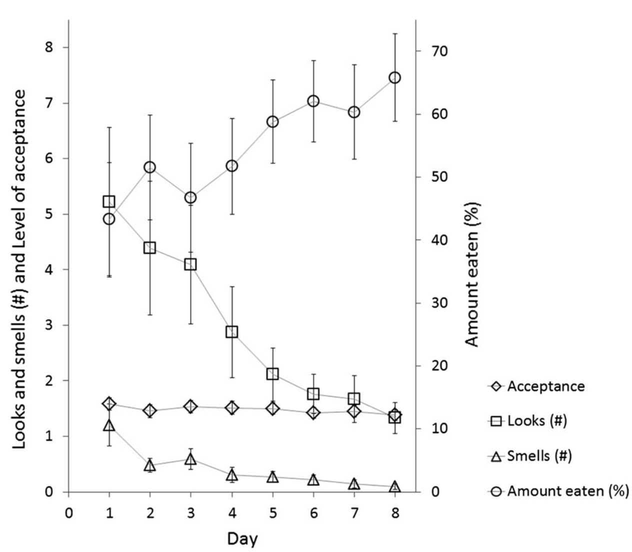

Fig. 1 Effect of repeated exposures on acceptance, consumption and exploration of novel food. *Error bars* SD/2

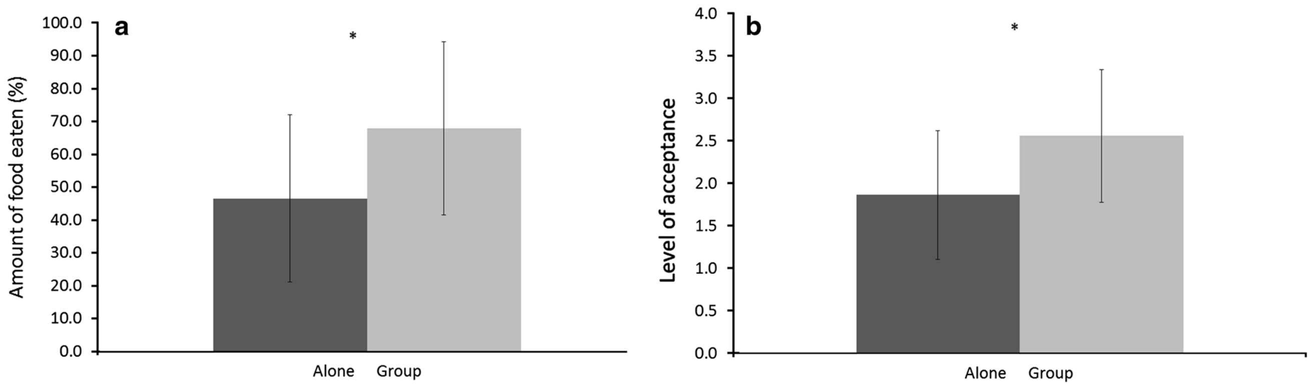

Fig. 2 Social influences on novel food. **a** Consumption: average amount eaten in percentage. **b** Acceptance: average level of acceptance when alone or when in a group. 1 = refusal of the food item; 3 = acceptance of the food item. *Error bars* SD

in explorative behaviour (Visalberghi et al. 1998). Nevertheless, after repeated exposures, orangutans did not increase acceptance of novel items.

Due to the design of the experiments, external distraction could not have influenced our results. Contrasting with our predictions, repeated exposures over 8 days did not increase acceptance, even if the captive individuals may have been considered disengaged. Our results did not show a trend ($p = 0.15$), which means that even when offering the same rejected item for periods longer than that involved in the experiment would likely not yield any substantial increase in acceptance. This experimental setting was set out to mimic natural forest conditions where an individual encounters an item and continues travelling afterwards. In other words, an orangutan would never be exposed for hours to a rejected item. This condition may however be brought about in captivity, where rejected items can be left in the enclosure of an individual. It remains to be assessed whether under this situation individuals would then eventually investigate said item. In summary, our results suggest that after an orangutan refuses a food item, it is unlikely he will later accept it even after repeated exposures. However, when orangutans accept a food and there are no apparent negative effects (e.g. nausea) thereafter, they will tend to gradually increase the amount eaten of that item.

The findings on the effects of sociality show that orangutans' acceptance and consumption of food items increase when in the presence of conspecifics, as compared to when alone. That is, when orangutans refused some food items when alone, they instead consumed these same food items when with others. Thus, acceptance only increased when orangutans were with other feeding conspecifics. Sociality effects on the increase of acceptance of novel food has been shown in other nonhuman primates, such as capuchin monkeys (Visalberghi and Fragaszy 1995), baboons (*Papio ursinus*; Cambefort 1981) and marmosets (*Callithrix jacchus*; Yamamoto and Lopes 2004; Voelkl et al. 2006), and chimpanzees (*Pan troglodytes*; Finestone et al. 2014). These results suggest that caution towards novel food is reduced in the presence of peers, who also simultaneously consume that food.

Under natural conditions, infant orangutans learn their diet via transmission of information from their mothers (Jaeggi et al. 2010). After achieving independence, social feeding occurs occasionally in wild orangutans (Sugardjito et al. 1987; te Boekhorst et al. 1990; Utami et al. 1997; Knott 1998) and is suggested to enhance the acquisition of foraging skills (van Schaik et al. 1999). If mothers are not present, as is the case for virtually all reintroduced animals, orangutans may choose other individuals as demonstrators (Russon and Galdikas 1995). This trend is seen in reintroduced orangutans, in which an increase in foraging efficiency is found as a result of social interactions with conspecifics (Riedler et al. 2010). Thus, as verified by our results, sociality may be of great importance for rehabilitant individuals. Social feeding yielded an increase in acceptance and consumption of novel foods, while simultaneously offering opportunities for the transmission of relevant food information between peers. This transfer of information may represent an additional benefit for reintroduced orangutans to feed together and offers the potential to further accelerate adaptation to an unfamiliar forest.

Increased acceptance of novel food leads to its incorporation in the diet of orangutans, a critical factor to maintain dietary diversity and ecological resilience. Hence, the higher the rate of novel food acceptance, the longer a reintroduced individual may assure its own survival across annual fluctuations in food availability, which across orangutan habitat is relatively intense (see Hardus et al. 2013). In wild populations, it is well established that the quality of fallback foods determines the carrying capacity of that habitat for an orangutan population (van Schaik et al. 2001; Wich et al. 2004; Marshall et al. 2009; Morrogh-Bernard et al. 2009). Reintroduced populations may however never fully reach the carrying capacity of their release site, as long as individuals do not take in important fallback foods, which may still remain unproven after several years of forest living (Russon 2002; Russon 2009; Russon et al. 2009). Captive training with the specific aim of increasing acceptance of important food sources by individuals before release may thus represent a determinant aspect of effective rehabilitation.

Increased consumption of novel food is additionally important in the process of adaptation to an unfamiliar forest. After an orangutan has accepted and incorporated a novel food into its diet, it is likely that it will start to consume it more often. Nevertheless, it is crucial that individuals learn to consume this food in sufficient quantities within relatively short periods (i.e. a season) so that they may endure potential periods of scarcity. Thus, the combination of these two factors—increased acceptance and consumption—is most favourable for rehabilitants to enrich their diet with important novel sources after release.

Recommendations for reintroduction

We suggest reintroduction programmes to present rehabilitant orangutans repeatedly with key food sources that are available in their intended release sites. Orangutans are suggested to categorise food, and this may help to introduce important sources based on the similarity of an established category (Russon 2002). If a rehabilitant is not accepting these items, we suggest presenting the food to the individual in a group (≥2 orangutans). This may reduce their caution towards the novel food, while the presence of knowledgeable individuals in the group likely assists the facilitation of the transmission of food-related information and/or skills. These actions will likely augment and diversify the diet of rehabilitants and increase survival probabilities after release. From the perspective of conservation effectiveness, this is a relatively small effort relative to the large financial and logistic investments required to rescue individuals, maintain quarantine facilities and release them into the wild (e.g. Rijksen and Meijaard 1999). These recommendations are relevant for all great ape species and possibly for other species with a high dietary diversity as well.

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