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ORIGINAL ARTICLE

Food washing and placer mining in captive great apes

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Abstract Sweet potato washing and wheat placer mining in Japanese macaques (*Macaca fuscata*) are among the most well known examples of local traditions in non-human animals. The functions of these behaviors and the mechanisms of acquisition and spread of these behaviors have been debated frequently. Prompted by animal caretaker reports that great apes [chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo abelii*)] at Leipzig Zoo occasionally wash their food, we conducted a study of food washing behaviors that consisted of two parts. In the first part we assessed the current distribution of the behavior on the basis of caretaker reports. In the second (experimental) part, we provided subjects individually with a water basin and two types of food (apples and cereal) that was either clean or covered/mixed with sand. We found that subjects of all species (except gorillas) placed apples in the water before consumption, and that they did so more often when the apples were dirty than when they were clean. Several chimpanzees and orangutans also engaged in behaviors resembling wheat placer mining.

Keywords Food washing · Placer mining · Tradition · Great apes

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Introduction

Sweet potato washing and wheat placer mining in Japanese macaques (*Macaca fuscata*) on Koshima Island are historically among the first proposed examples of local traditions in non-human animals (Kawamura 1959; Kawai 1965; for reviews see Itani and Nishimura 1973; Nishida 1987; Hirata et al. 2001). In 1954, the individual Imo of the Koshima troop was first observed washing a sweet potato in water before consumption, and over the following years, the behavior gradually spread to other members of the group, at first from the inventor to its close kin and playmates, and then from these early adopters to their offspring (e.g. Kawai 1965). A similar propagation pattern marked the spread of a second local tradition, wheat placer mining. In wheat placer mining, the macaques gather up grains and sand from the Koshima beach, throw the mixture into the water, and pick the floating grains from the water surface while the sand sinks to the bottom—thereby separating grains and sand much more efficiently than by picking them up from the sand one by one (Kawai 1965; Hirata et al. 2001).

One question with regard to food washing and placer mining behaviors concerns to what extent and under which conditions other (primate) species are capable of acquiring them. While, to the authors' knowledge, the only existing reports of placer mining come from the Koshima troop and from the experimental study of food washing by Visalberghi and Fragaszy (1990), there is a variety of reports of food washing techniques being acquired by individuals, both captive and in the wild, in other troops of Japanese macaques (Kawai 1965; Scheurer and Thierry 1985; Nakamichi et al. 1998), and other monkey species, such as crab-eating macaques (*Macaca fascicularis*; Wheatley 1988; Visalberghi and Fragaszy 1990), wedge-capped

capuchins (*Cebus olivaceus*; Urbani 2001), and tufted capuchins (*Cebus apella*; Visalberghi and Fragaszy 1990). There are, however, with very few exceptions, hardly any reports of food washing in great ape species (see Bermejo et al. 1994 for a report of washing in wild bonobos, though the authors did not specify what they exactly meant by "washing"). While this lack of observational evidence may simply reflect the fact that the diet of great apes predominantly consists of food that does not need to be cleaned before consumption, it remains an interesting question whether great apes may acquire food washing behaviors if environmental properties create a pressure to do so. Great apes are known to engage in a variety of activities involving water (for a review of water-related behaviors including all great ape species see Kempf 2009). Moreover, chimpanzees and orangutans are particularly innovative when dealing with water and they use it for different functions, both in the wild (e.g. Boesch 2003; Russon et al. 2010) and in captivity (Mendes et al. 2007; Tennie et al. 2010; Hanus et al. 2011).

A second question with regard to food washing and placer mining concerns the function of the behaviors. This question arose due to the emergence of different behavioral variants involving sweet potatoes and water (e.g. cleaning vs seasoning, see Kawai 1965; Watanabe 1994; Hirata et al. 2001). So far, it appears that both explanations might be correct, as both behaviors ("washing in freshwater" and "dipping in salt water") occurred (sometimes even together) in multiple individuals and still did even 40 years after the original observations (Kawai et al. 1992; Watanabe 1994; Hirata et al. 2001). The function of placer mining in Japanese macaques is less controversial. It is a time-efficient method that separates the grains from the sand (Hirata et al. 2001) which is advantageous since consuming too much sand might wear out the monkeys' teeth (Watanabe 1994). It should also be noted that another function of placing food items in water that has been suggested for certain bird species is moistening (e.g. Morand-Ferron et al. 2004).

A third question with regard to food washing and placer mining behaviors concerns the extent to which different modes of behavior acquisition (individual learning vs imitation or other types of social learning) contribute to the propagation patterns of the behaviors as observed in the Koshima troop and other groups of monkeys (Kawai 1965; Itani and Nishimura 1973; Galef 1990, 1992, 2004; Visalberghi and Fragaszy 1990; Lefebvre 1995; Tomasello and Call 1997; Reader 2004).

The current investigation was prompted by animal caretakers reporting that individuals of different groups of captive great apes at Leipzig Zoo would occasionally "wash" their food in their enclosures. Reportedly, particular individuals of each group of apes housed at Leipzig Zoo [one group of bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo abelii*) each, and two groups of chimpanzees (*Pan troglodytes*)] would take food that was provided to them by the caretakers during feeding times to bodies of standing water and throw or dunk them into the water before consumption. For some individuals it was reported that they had been doing this for many years. In contrast, there were no reports by any caretaker that any individual had ever engaged in anything resembling wheat placer mining, even though the apes have on occasion access to food comparable to grain, such as barley, dried pieces of corn, wheat, sorghum, and oat.

This study aimed at: (a) establishing the prevalence of food "washing" behavior in the different groups, based on caretaker reports as well as overt "washing" behavior in an experimental context, (b) exploring whether great apes would exhibit placer mining behavior in an experimental context, (c) investigating the function of placing food in water (to determine whether the label "washing" is justified) and, if exhibited, placer mining behavior. For assessment of the initial distribution of food "washing" within the different groups, all caretakers were administered a questionnaire in which they reported whether they had ever seen certain individuals engage in food washing or placer mining. In the experimental study that followed, the subjects of all species (gorillas, chimpanzees, orangutans, and bonobos) were exposed to a water basin and one of four different types of food: clean apples, dirty apples, plain chocopops cereal, or a mixture of chocopops cereal and sand.

Methods

Assessment of initial distribution of "food washing" and "placer mining"

Subjects

In order to assess the initial distribution of food washing, all caretakers ($N = 13$) were administered a set of questionnaires several weeks prior to the experimental study. The caretakers rated 48 apes from five different groups (bonobos, gorillas, orangutans, and two chimpanzee groups) housed at Wolfgang Köhler Primate Research Center in Leipzig Zoo, Germany. Among the apes rated were 24 chimpanzees [18 individuals in the large group, including 7 males and 11 females, mean age in years $M = 18.17$, standard deviation (SD) 12.19, as well as 6 individuals in the small group, including 1 male and 5 females, mean age $M = 13.33$, SD = 4.03], 8 bonobos (4 males, 4 females, mean age $M = 11.19$, SD = 8.64), 6 gorillas (1 male, 5 females, mean age $M = 14.17$,

SD = 12.73), and 10 orangutans (3 males, 7 females, mean age $M = 10.48$, SD = 10.30).

Questionnaires

Semi-standardized, individual interviews were conducted with all caretakers by a single interviewer (M.A.) who filled out the questionnaires. First, a precise definition of food washing was read to the caretakers. They were told that instances were considered food washing if and only if one and the same individual had been seen taking a dirty piece of food (such as a piece of vegetable covered in sand) to a source of water, throwing or dunking it into the water, taking it out, and subsequently eating it. Caretakers were asked for each individual from all groups with which they had frequent contact whether they had ever seen that individual handle food in the described fashion. They could answer with either "yes", "no", or "not sure". If they answered "yes", they were also asked whether they could remember when they had seen it for the first time. All caretakers were asked to rely on their own memory only and not to talk to each other about the interview during the period of data collection. At the end of the questionnaire the caretakers were given the chance to report orally anything they thought of as possibly interesting with regard to food washing behavior. A second questionnaire to assess potential instances resembling wheat placer mining was administered to the caretakers in the same semi-standardized interview format. Caretakers were read a description of the behavior as reported for the Japanese macaques of Koshima Island. They were told that some of these animals "throw pieces of grain which are too dirty for immediate consumption into water, with the result that the sand will sink and the clean grain floats on the water surface and can be picked out and consumed by the animal". Caretakers were then asked whether they had ever seen any individual engaging in this or a similar behavior with pieces of grain, muesli, or a comparable food, again with the constraint that one and the same individual carried out all steps of the behavioral sequence.

Experimental study

Subjects

All great apes housed at Wolfgang Köhler Primate Research Center in Leipzig Zoo, Germany, participated in the experimental study. This included 24 chimpanzees (6 males and 12 females tested alone, and 3 females tested with dependent offspring), 6 gorillas (1 male and 3 females tested alone, and 1 female with dependent offspring), 8 bonobos (3 males tested alone, and 2 females tested with dependent offspring), and 10 orangutans (1 male and 1 female tested alone, and 4 females tested with dependent offspring or relative). For the pairs or triads in which females were tested together with dependent offspring or relative, only cases in which one party monopolized all apples could be included in data analysis. If instead one party did not monopolize all of the apples (leaving the subjects' data impossible to compare to individually tested subjects), all data for this pair or triad was excluded from further analysis. This affected all chimpanzees and bonobos who were tested together with dependent offspring, as well as one orangutan and her adopted sister, leaving a total of 31 individuals who actively participated in the experiment to further analysis: 18 chimpanzees (6 males, 12 females, mean age $M = 16.67$, SD = 9.32), 3 bonobos (3 males, mean age $M = 18.00$, SD = 7.81), 5 gorillas (1 male, 4 females, mean age $M = 16.60$, SD = 12.58), and 5 orangutans (1 male, 4 females, mean age $M = 18.00$, SD = 9.03). One bonobo did not participate in the second part of the experiment (chocopops cereal conditions), because he was transferred to another zoo, therefore only two bonobos were tested in these conditions (2 males, mean age $M = 20.00$, SD = 9.90).

The apes who participated in this study have regular access to semi-natural indoor and outdoor enclosures equipped with natural vegetation, ropes, and enrichment items, and to sleeping and retreat rooms. In the indoor and outdoor enclosures the apes also have access to bodies of standing water such as small ponds or trenches. The apes are fed several times per day and have drinking water at free disposal. Their regular diet consists of fruit, vegetables, and animal food such as banana pellets. During feeding, food is sometimes thrown into the water by the keepers (see "Results"). All apes participate in cognitive studies on a regular basis, including other on-going studies during the time this study was conducted. Participation in all studies is voluntary. All studies are non-invasive and the apes are never deprived of food or water.

Materials and procedure

All tests were conducted in the ape sleeping rooms. All subjects were tested individually or together with dependent offspring and could not see each other during testing. Every subject was exposed to four different conditions in which he or she always had access to a water basin, and one of two different foods (either apples or chocopops cereal) which were either dirty (experimental conditions) or clean (control conditions, see Fig. 1). The water basin was a black steel container (50 cm × 20 cm × 30 cm) which was attached to one of the mesh doors in the sleeping room and was filled with approximately 20 l of water (see Fig. 2). This water basin was unfamiliar to the apes prior to the study.

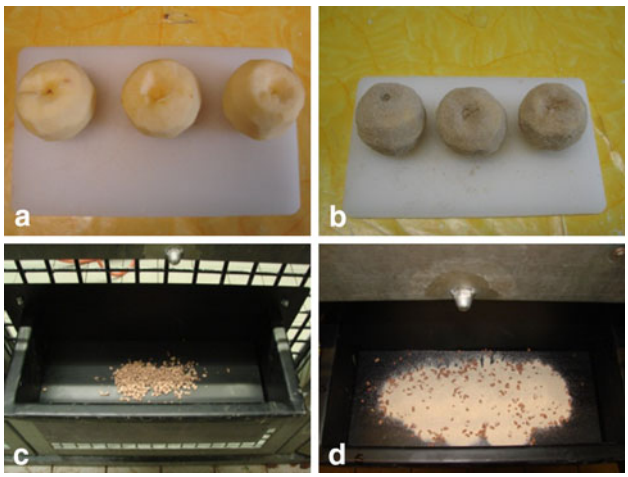

Fig. 1 Food used in the experimental and control conditions: **a** clean apples, **b** dirty apples, **c** clean chocopops cereal, **d** chocopops cereal–sand mixture

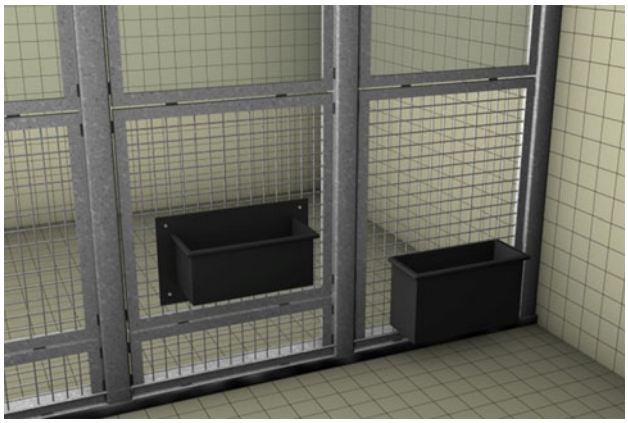

Fig. 2 Experimental setup in chocopops cereal conditions: water basin (*right*) and second basin containing sand and/or chocopops cereal

In the apple conditions, three small apples (120–130 g) of the variety Gala Royal and Gala were used. Apples were placed on the floor in a line, with approximately 20 cm space between two apples and an equal distance of approximately 75 cm between the water basin and each apple. In the clean apples condition, apples were peeled before they were placed in the cage; in the dirty apples condition, they were peeled and sprinkled from all sides with dry, fine-grained quartz sand until they were completely covered from all sides (see Fig. 1b).

In the chocopops cereal conditions, a German cereal with the brand name Crownfield Choco Rice was used as food. In the clean chocopops cereal condition, 12.5 g of this cereal (approximately 300–350 pieces of cereal) were placed in a second basin (50 cm × 20 cm × 15 cm) which was installed in close proximity (a distance of approximately 30 cm) to the water basin (see Fig. 2); in the dirty chocopops cereal condition a mix of 12.5 g of this cereal and 500 g of sand (the same that was used in the apple conditions) were placed in the second basin (see Fig. 1d).

After the food was in place, the subject was let into the testing room and coding and timing started once the ape entered the room. In the apple conditions, behavior coding continued until the subject had either consumed all three apples or after a maximum of 10 min had elapsed. In the chocopops cereal conditions, behavior coding continued for 10 min or until the subject had consumed more than 95 % of all chocopops cereal (clean condition only). Then the ape was let out and was free to take any leftover food with him/her. If during the session the water was polluted or contaminated in any way, the water was cleaned and/or replaced with fresh water for the next trial. The room was cleaned of all visible residual pieces of food before baiting it again and letting the next subject in. During testing the subjects did not receive training, encouragement, or demonstration of any kind. All sessions were videotaped with one fixed camera focusing on the water basin and one or two cameras held by the experimenters following all movements of the subject and its interactions with the food and the water.

Experimental design

The study was conducted between July 2010 and February 2011. All tests were conducted in the morning hours between 8.30 and 12.30. Subjects never completed more than one trial per day. All individuals were tested in blocks of food condition, that is, they were tested in one food condition first (e.g. apples) and then, after a break of several weeks, in the other condition (e.g. chocopops cereal).

All subjects completed four trials of each of the four conditions, so that each individual completed 16 trials. In order to control for possible order effects, all chimpanzees were allocated to one of four groups which counterbalanced the order of conditions (groups I and II starting with apples and groups III and IV starting with chocopops cereal; groups I and III starting with dirty food and groups II and IV starting with clean food). For practical reasons, for the other species a simpler design had to be used, always starting with the apple conditions and counterbalancing for clean versus dirty food only (groups I and II). For each species, the groups (defining the order of conditions) were matched for the following variables: age, sex, housing group membership (for the chimpanzees), rank (high, medium, or low rank positions based on averages of linear rank assignments provided by caretakers and research assistants), and the number of individuals who already had a reputation for washing food (as assessed in the caretaker interviews conducted prior to the experimental study). The matching of groups was only

marginally affected by the exclusion of some individuals from the data analysis described above.

Data analysis and scoring

In the apple condition, the dependent variables were the number of apples eaten, the number of apples "washed", and the number of apples "washed" and eaten by an individual in the course of each trial (zero, one, two, or three). An apple counted as eaten if the subject had started feeding on it, that is, if it had bitten off a considerable amount. An apple counted as "washed" if the apple was placed in the water before the subject had fed on it. Placing in water was defined as the subject dipping, dunking, or releasing the apple into the water. In the chocopops cereal condition, the main dependent variables were whether any amount of chocopops cereal or chocopops cereal–sand mixture was eaten, whether any amount of chocopops cereal or chocopops cereal–sand mixture was placed in water and whether any amount of chocopops cereal or chocopops cereal–sand mixture was placed in water and subsequently eaten ("placer mining"), with all of these variables coded "one" if the behavior occurred, and "zero" otherwise. Placing in water was defined as placing any amount of chocopops cereal or chocopops cereal–sand mixture in the water using hands or feet. Placer mining was coded if the subject subsequently took floating chocopops cereal out of the water and ate them (either after scooping them up with hands or feet or by feeding directly from the water surface). In order to obtain a conservative estimate of placer mining behavior, it was not coded as placer mining if the subject spat chocopops cereal or chocopops cereal–sand mixture into the water or if some chocopops cereal or chocopops cereal–sand mixture dropped into the water as a result of the subject feeding with its head above the water basin or dipping its snout into the water basin while having its mouth full.

A second rater coded 32 of the apple condition trials (12.9 % of all trials) and 47 of the chocopops cereal condition trials (19.58 % of all trials) to assess inter-observer reliability. The trials were randomly selected, balancing for species and conditions (clean vs dirty). Since for the chocopops cereal condition the amount of trials in which the first rater coded "chocopops cereal washed and eaten" was extremely low (16 trials altogether), all of these and an additional random 31 trials coded "chocopops cereal not washed and eaten" were selected for reliability coding. For the apple condition, inter-observer agreement, as reflected by Kendall Tau-b, was perfect ($\tau_b = 1.00$ for number of apples eaten, for number of apples washed, and for number of apples washed and eaten). For the chocopops cereal condition, Cohen's Kappa indicated high inter-observer agreement for whether chocopops cereal were: eaten ($\kappa = 1.000$), placed in water ($\kappa = 0.902$), placed in water and eaten ($\kappa = 0.902$), that is, whether placer mining had occurred. There were only two cases in which the two raters did not agree on whether chocopops were thrown in the water and subsequently eaten. These two instances were then coded by a third rater and the data was updated before analysis according to which coding (e.g. whether placer mining did or did not occur) two of the three raters agreed upon.

Exact Wilcoxon signed-rank tests were conducted to compare the amount of apples eaten, the amount of apples washed, and the number of trials in which placer mining occurred, between clean and dirty conditions. To analyze whether there were any differences between species in the amount of apples washed or the number of trials in which placer mining occurred in either condition, exact Kruskal–Wallis tests were conducted. In cases in which such differences were found, subsequent pairwise comparisons were run (exact Mann–Whitney U tests). To analyze for relationships between occurrences of food washing in the experiment and keeper reports of food washing, as well as occurrences of placer mining in the experiment, Fisher's exact tests were conducted. All statistical analyses were two-tailed.

Results

Caretaker reports

For each individual who was identified as having washed food in the past, Table 1 lists the number of caretakers who reported having seen this individual wash food. For all five groups caretakers reported having seen food washing behavior in two or more individuals. In all groups, except gorillas, there was at least one individual for which there were reports of food washing from at least two different caretakers. In contrast, there was not a single report of behaviors resembling placer mining for any individual by any caretaker. Among the additional comments made by the caretakers, the most interesting (with regard to the experimental study) included that: (a) food is thrown into the water by some of the keepers on purpose to keep the apes occupied, and (b) a lot of animals clean their food manually by brushing it on their arms or on their chin.

Experimental study

Apple washing

Twenty-one subjects (13 chimpanzees, 3 bonobos, 5 orangutans) exhibited food washing behavior as defined above. Of the clean and dirty apples that were "washed" as

Table 1 Caretaker reports of food washing behavior

Group	Number of animals (*N*)	Number of raters (*N*)	Animals identified as food washers	Sex	Age	Number of caretakers who reported food washing[a]	Time of first observation
Chimpanzee A	18	5	Corrie	Female	33	1	At least since 2006
			Natascha	Female	30	2	At least since 2006
			Patrick	Male	13	1	2010
			Swela	Female	14	1	2007 or later
Chimpanzee B	6	3	Alex[b]	Male	9	1	Before 2004
			Alexandra[b]	Female	10	3	Before 2004
			Annett[b]	Female	10	3	Before 2004
			Fifi	Female	17	3	At least since 2007
			Jahaga	Female	17	1	Not sure
Bonobos	8	5	Joey	Male	27	2	Since 2001
			Kuno	Male	13	3	Since 2001
			Limbuko[b]	Male	14	5	Since 2001
			Ulindi[b]	Female	16	5	Since 2001
			Yasa[b]	Female	12	3	Since 2001
Orangutans	10	6	Dokana	Female	21	1	At least since 2004
			Kila	Female	10	2	Since 2008
			Padana	Female	12	5	Since 2001
			Pini	Female	22	3	Since 2008
			Raja	Female	6	3	Since 2009
Gorillas	6	5	Kibara	Female	6	1	Not sure
			Viringika[b]	Female	15	1	Not sure

[a] Instances of keepers rating "not sure" (5.33 % of all ratings) were not considered

[b] Additional report of food washing behavior by one or more caretakers who reported having relatively little contact with the group

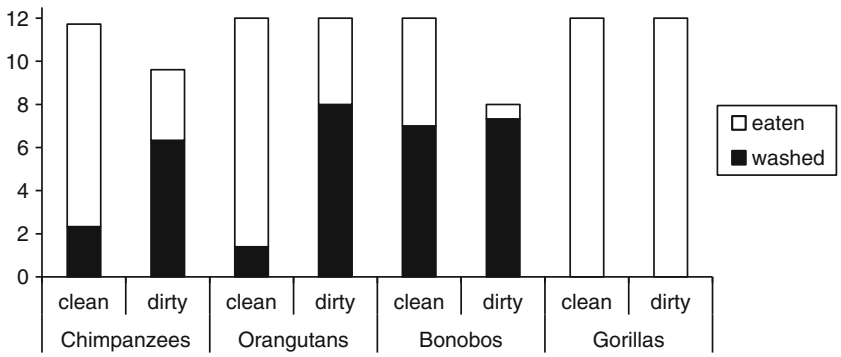

Fig. 3 Mean number of apples eaten and apples that were placed in water ("washed") in both conditions, listed for each species

defined (dunked, dipped, or released into the water), 98.57 and 99.43 % were subsequently eaten, respectively. Subjects washed significantly more apples in dirty compared to clean condition (Wilcoxon $T = 2$, $N = 31$, $P < 0.001$; clean: $M = 2.26$, SD = 3.79; dirty: $M = 5.68$, SD = 5.46; see Fig. 3). Only one of the subjects exhibited washing in the clean condition only and never in the dirty condition. There was an effect of species for the amount of apples placed in water in the dirty condition [exact Kruskal–Wallis test, $\chi^2(3) = 8.258$, $P = 0.028$], but not for those in the clean condition [$\chi^2(3) = 5.607$, $P = 0.120$]. Pairwise comparisons (exact Mann–Whitney U tests) revealed that the chimpanzees ($U = 15.0$, $N_{Ch} = 18$, $N_{Go} = 5$, $P = 0.022$), the bonobos ($U = 0.0$, $N_{Bo} = 3$, $N_{Go} = 5$, $P = 0.018$), and the orangutans ($U = 0.0$, $N_{Or} = 5$, $N_{Go} = 5$, $P = 0.008$) placed dirty apples in water significantly more often than gorillas (who never showed any food washing behavior).

All subjects ate apples in at least one trial. There were no significant differences in the number of apples eaten between clean and dirty condition (Wilcoxon $T = 0$, $N = 31$, $P = 0.063$; clean: $M = 11.84$, SD = 0.73; dirty: $M = 10.23$, SD = 4.14). Note that the standard deviation of apples eaten is considerably larger for the dirty condition, reflecting the fact that 5 of the 31 individuals only ate zero to three apples across all trials of the dirty condition, whereas all other subjects ate all 12 apples in the dirty condition. There were no significant species differences in the amounts of apples eaten in clean condition [exact Kruskal–Wallis test, $\chi^2(3) = 1.493$, $P = 1.000$] or dirty condition [$\chi^2(3) = 3.126$, $P = 0.380$].

Subjects who did not exhibit any food washing as defined (5 chimpanzees, and all 5 gorillas) ate all of the apples in clean condition, but only eight of them ate all of the apples in dirty condition. When subjects did not place food in water before consumption, they often nonetheless cleaned the apples in various ways, including brushing the apples with their hands, on their bodies or chins, scraping the sand off with their fingers, biting, or sucking the sand off the apples and spitting it out, breaking the apples, rolling the apples across the cage floor, or rubbing them on the cage mesh.

Chocopops placer mining

Seven subjects (4 chimpanzees and 3 orangutans) placed chocopops in water as defined above. Of the trials in which chocopops (and sand) were thrown into the water (14 in dirty condition and 1 in clean condition), in 93.33 % of cases the food was subsequently eaten, that is, genuine placer mining occurred. The difference between the number of trials in which chocopops were thrown into the water for clean chocopops versus chocopops mixed with sand was not significant (Wilcoxon $T = 2$, $N = 30$, $P = 0.063$; clean: $M = 0.03$, SD = 0.18; dirty: $M = 0.47$, SD = 1.07). All subjects threw chocopops (and sand) into the water in the dirty condition only, except one female chimpanzee that did so once in the clean condition (without subsequently consuming the floating chocopops). Species did not significantly differ in their tendency to exhibit placer mining in the clean condition [$\chi^2(3) = 0.667$, $P = 1.000$] or the dirty condition [exact Kruskal–Wallis test, $\chi^2(3) = 7.077$, $P = 0.074$].

All subjects except one ate chocopops in at least one trial. Subjects ate chocopops significantly more often in clean than in dirty condition (Wilcoxon $T = 0$, $N = 30$, $P = 0.016$; clean: $M = 3.73$, SD = 0.83; dirty: $M = 3.17$, SD = 1.49). There were no significant species differences in the number of trials in which chocopops were eaten in clean condition [exact Kruskal–Wallis test, $\chi^2(3) = 2.957$, $P = 0.525$], or dirty condition [$\chi^2(3) = 2.729$, $P = 0.479$].

Of the 23 subjects who did not exhibit any placer mining as defined (14 chimpanzees, 2 bonobos, 2 orangutans, and all 5 gorillas) all but one ate chocopops in some trials of the clean condition, and all but three ate chocopops in some trials of the dirty condition. When subjects did not exhibit placer mining in the chocopops trials, they engaged in different eating techniques, such as picking out chocopops one by one with hands or tongue, spreading the mixture on the cage floor and subsequently picking them out, or simply eating both chocopops cereal and sand from the basin.

Relationship between both behaviors

Except for one subject (chimpanzee Lome), all individuals who placed food in water in the chocopops conditions also placed food in water in the apple conditions. Of these six subjects (who exhibited both behaviors), all but one (chimpanzee Natascha) were exposed to the chocopops condition after completing the apples condition. However, 14 other subjects who exhibited food washing behavior never exhibited any placer mining behavior (7 chimpanzees that completed the chocopops conditions first and 3 chimpanzees, 2 orangutans, and 2 bonobos who completed the apple conditions first). The relationship between food washing (exhibited vs not exhibited) and placer mining (exhibited vs not exhibited) was not statistically significant (Fisher's exact test, $P = 0.372$, two-tailed).

Since only the chimpanzee groups were fully counterbalanced for the order in which they received food of either type (apples vs chocopops), the analysis of possible food order effects was carried out for chimpanzees only. Mann–Whitney U tests revealed no significant differences in amount of clean ($U = 39.5$, $N_{Ap} = 8$, $N_{Ch} = 10$, $P = 1.000$) or dirty ($U = 26.5, N_{Ap} = 8, N_{Ch} = 10, P = 0.240$) apples that were washed as a function of food order (apples first vs chocopops first). Likewise, there was no effect of food order on the number of trials in which placer mining was exhibited in the dirty chocopops condition (Mann–Whitney U test, $U = 33.0$, $N_{Ap} = 8, N_{Ch} = 10, P = 0.330$).

Caretaker reports and experimental data

Table 2 shows the relationship between keeper assessments of food washing propensity (none vs one or more keeper

Table 2 Relationship between keeper reports and food washing in experiment

		Experimental study: subject washed food	
		Yes	No
Keeper reports: "subject has washed food"	Yes	14	4
	No	7	6

reports) and behavioral data from the experimental study ("never washed food" vs "washed food in at least one trial"). There was some overlap, but there were also considerable incongruities between keeper reports and behavior in the experimental study. Accordingly, Fisher's exact test of this relationship was not significant ($P = 0.247$, two-tailed).

Discussion

Both the caretaker assessment and the subsequent experimental study established that food washing was prevalent in all captive groups of great apes, except gorillas. In all groups, except gorillas, there was at least one individual for which two or more caretakers reported that they had seen this individual engage in food washing in the past (three individuals in the small chimpanzee group, one individual in the large chimpanzee group, five individuals in the bonobo group, and four individuals in the orangutan group). Some of these individuals were reported to have engaged in the behavior for many years. Additionally, 13 chimpanzees, three bonobos, and five orangutans (but none of the gorillas) exhibited food washing in the experiment. This study shows that individuals of these species wash food under solitary conditions. Larger sample sizes and possibly more experience are necessary to determine whether the complete lack of evidence for food washing in gorillas represents a mere artifact of this study or rather a general cognitive limitation of this species.

Not a single caretaker had identified even one subject as having ever engaged in any behavior resembling wheat placer mining before the experimental study was conducted, even though the groups have, on occasion, access to food comparable to the wheat grains on Koshima Island. Yet, within a few sessions, several chimpanzees and orangutans exhibited behaviors that resembled the placer mining behavior of the Koshima monkeys. While the role that social context plays in the propagation of local traditions like food washing and placer mining has been well established for a variety of behaviors in a range of primate species (e.g. Nahallage and Huffman 2007; Huffman et al. 2010), we tentatively interpret the spontaneous acquisition of placer mining behavior in multiple individuals that could not observe each other and had, to the best of our knowledge, no prior experience with this behavior, as evidence that individual exploration and inventiveness also play an important role in the emergence of placer mining.

With regard to the function of placing food in water, there was a selectivity effect in the experimental study: more food was thrown into the water in the dirty apples condition than in the clean apples condition. Since it is implausible that placing the food in water served the purpose of moistening it (in which case dunking equal amounts of clean and dirty food would be expected), or seasoning it (since only fresh water was used), we conclude that placing food in water served the purpose of cleaning (ergo washing) it. With regard to the placing of food in water in the chocopops condition, due to the very low number of occurrences (15 out of 240 trials) it is too early to tell whether this behavior is selective in the same way food washing was in this study—which would indicate that the function of the behavior is to clean the food. Although for the placer mining subjects, the behavior did not occur in all trials with the chocopops cereal–sand mixture, and was in some individuals alternated with other techniques of food consumption, it is intriguing that genuine placer mining (including the consumption of floating chocopops), albeit very rare, was restricted to the dirty chocopops condition.

There are hardly any reports of food washing or similar behaviors in great apes in the wild. This may simply be explained with the fact that the diet of great apes consists predominantly of food found in the forest canopy—the pressure to wash food and opportunities to do so are quite rare. Yet, in this experiment, individuals of all species (except gorillas) placed food items in water, and some chimpanzees and orangutans even exhibited behaviors resembling placer mining behavior. This finding is in accordance with the argument put forward by Visalberghi and Fragaszy (1990) that food washing is a relatively easy task to learn and may emerge frequently under favorable conditions (such as affordances and leisure time provided in captivity).

There was a considerable incongruence between, on the one hand, caretaker ratings of which animals wash food and, on the other, overt food washing behavior in the experimental study. Group pressure (monopolization of water sources by dominant individuals, risk of kleptoparasitism) might explain why some individuals who acquired and exhibited food washing behavior in the experiment had not shown it frequently in their enclosure in the past (see Visalberghi and Fragaszy 1990; Drea and Wallen 1999; Morand-Ferron et al. 2004; Lonsdorf and Bonnie 2010). Moreover, some individuals who had been reported to wash food never exhibited this behavior in the experiment. One reason might be that the two situations (water source in enclosure vs water basin in testing cage) were perceived very differently by these individuals and made it more difficult, or less compelling, for them to engage in food washing behavior in the experimental situation. There is some evidence that even very subtle changes in experimental/environmental conditions may impact whether a behavior is expressed or not (e.g. Mulcahy and Call 2006; Tennie et al. 2006; Hanus et al. 2011).

Ten individuals (five chimpanzees and all tested gorillas) did not place any apples in the water. Cognitive differences between individuals (or, in the case of gorillas, species) may account for this inability to acquire the behavior, or at least for slower learning rates. Thus, these individuals might have benefitted from more experience with the task. Motivational differences may also account for the absence of food washing in some individuals. Since most individuals who did not wash the dirty apples nevertheless ate them, the pressure to clean the food thoroughly might just not have been great enough to elicit washing behavior.

Why did only a few individuals exhibit placer mining behavior while so many others did not? First, as with food washing, it might be that either some subjects need more time to learn and might have benefitted from more experience with the task, or the chocopops cereal was simply not dirty enough to discourage other techniques of consumption (such as picking out the chocopops or eating both chocopops and sand). Second, it is worthy of note that placer mining also occurs less frequently in the Japanese macaques of Koshima than does sweet potato washing (Kawai 1965). This difference has been attributed to the fact that placer mining is more complex, requiring a different form of causal understanding and more behavioral inhibition from an individual (throwing away food before consuming it; Itani and Nishimura 1973; Nishida 1987; Kawai et al. 1992; Watanabe 1994). Thus, it is not surprising that there was also a difference in acquisition rates for the two behaviors in this study.

In conclusion, we showed that placing food in water before consumption occurred in captive chimpanzees, orangutans, and bonobos, and that this behavior was selective and could thus be called "washing". Furthermore, several chimpanzees and orangutans also engaged in behavior resembling wheat placer mining. Further research could illuminate to what extent these results can be generalized to other primate species, particularly gorillas, and whether behavior acquisition might be further facilitated by additional experience, as well as demonstrations of actions and results (cf. Tennie et al. 2010).

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References

Bermejo M, Illera G, Pí JS (1994) Animals and mushrooms consumed by bonobos (*Pan paniscus*): new records from Lilungu (Ikela), Zaire. Int J Primatol 16:879–898

Boesch C (2003) Is culture a golden barrier between human and chimpanzee? Evol Anthropol Issues News Rev 12:82–91

Drea CM, Wallen K (1999) Low-status monkeys "play dumb" when learning in mixed social groups. Proc Natl Acad Sci USA 96:12965–12969

Galef BG Jr (1990) Tradition in animals: field observations and laboratory analyses. In: Bekoff M, Jamieson D (eds) Readings in animal cognition. The MIT Press, Cambridge, pp 74–95

Galef BG Jr (1992) The question of animal culture. Hum Nat 3:157–178

Galef BG Jr (2004) Approaches to the study of traditional behaviors of free-living animals. Learn Behav 32:53–61

Hanus D, Mendes N, Tennie C, Call J (2011) Comparing the performances of apes (*Gorilla gorilla*, *Pan troglodytes*, *Pongo pygmaeus*) and human children (*Homo sapiens*) in the floating peanut task. PLoS One 6:e19555. doi:10.1371/journal.pone.0019555

Hirata S, Watanabe K, Kawai M (2001) "Sweet Potato Washing" revisited. In: Matsuzawa T (ed) Primate origins of human cognition and behavior. Springer, Berlin, pp 487–508

Huffman MA, Spiezio C, Sgaravatti A, Leca JB (2010) Leaf swallowing behavior in chimpanzees (*Pan troglodytes*): biased learning and the emergence of group level cultural differences. Anim Cogn 13:871–880

Itani J, Nishimura A (1973) The study of infrahuman culture in Japan. In: Menzel EW, Jr. (ed) Precultural primate behavior. Symposia of the fourth international congress of primatology, vol 1. Karger, Basel, pp 26–50

Kawai M (1965) Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. Primates 6:1–30

Kawai M, Watanabe K, Mori A (1992) Precultural behaviors observed in freeranging Japanese monkeys on Koshima islet over the past 25 years. Primate Rep 32:143–153

Kawamura S (1959) The process of sub-culture propagation among Japanese macaques. Primates 2:43–60

Kempf E (2009) Patterns of water use in primates. Folia Primatol 80:275–294

Lefebvre L (1995) Culturally-transmitted feeding behaviour in primates: evidence for accelerating learning rates. Primates 36:227–239

Lonsdorf E, Bonnie K (2010) Opportunities and constraints when studying social learning: developmental approaches and social factors. Learn Behav 38:195–205

Mendes N, Hanus D, Call J (2007) Raising the level: orangutans use water as a tool. Biol Lett 3:453–455

Morand-Ferron J, Lefebvre L, Reader SM, Sol D, Elvin S (2004) Dunking behaviour in Carib grackles. Anim Behav 68:1267–1274

Mulcahy N, Call J (2006) How great apes perform on a modified trap-tube task. Anim Cogn 9:193–199

Nahallage CAD, Huffman MA (2007) Acquisition and development of stone handling behavior in infant Japanese macaques. Behaviour 144:1193–1215

Nakamichi M, Kato E, Kojima Y, Itoigawa N (1998) Carrying and washing of grass roots by free-ranging Japanese macaques at Katsuyama. Folia Primatol 69:35–40

Nishida T (1987) Local traditions and cultural transmission. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsacker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 462–474

Reader SM (2004) Distinguishing social and asocial learning using diffusion dynamics. Learn Behav 32:90–104

Russon AE, Kuncoro P, Ferisa A, Handayani DP (2010) How orangutans (*Pongo pygmaeus*) innovate for water. J Comp Psychol 124:14–28

Scheurer J, Thierry B (1985) A further food-washing tradition in Japanese macaques (*Macaca fuscata*). Primates 26:491–494

Tennie C, Call J, Tomasello M (2006) Push or pull: imitation vs. emulation in great apes and human children. Ethology 112:1159–1169

Tennie C, Call J, Tomasello M (2010) Evidence for emulation in chimpanzees in social settings using the floating peanut task. PLoS One 5:e10544. doi:10.1371/journal.pone.0010544

Tomasello M, Call J (1997) Primate cognition. Oxford University Press, New York

Urbani B (2001) Food-washing among wedge-capped capuchin monkeys (*Cebus olivaceus*). Hum Evol 16:225–228

Visalberghi E, Fragaszy DM (1990) Food-washing behaviour in tufted capuchin monkeys (*Cebus apella*) and crabeating macaques (*Macaca fascicularis*). Anim Behav 40:829–836

Watanabe K (1994) Precultural behavior of Japanese macaques: longitudinal studies of the Koshima troops. In: Gardner RA, Gardner BT, Chiarelli B, Plooij FC (eds) The ethological roots of culture. Kluwer, Dordrecht, pp 81–94

Wheatley BP (1988) Cultural behavior and extractive foraging in *Macaca fascicularis*. Curr Anthropol 29:516–519