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ORIGINAL ARTICLE

An evaluation of the geographic method for recognizing innovations in nature, using zoo orangutans

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Abstract Innovation and social learning are the raw materials for traditions and culture. Of these two, innovation has received far less scrutiny, largely because of difficulties assessing the innovation status of behaviors. A recent attempt proposes recognition of innovations in natural populations based on assessment of the behavior's properties and its geographic and local prevalence. Here we examine the validity of this approach and the list of 43 potential innovations it generated for wild orangutans by extending the comparison to zoo orangutans. First, we created an inventory of the behavioral repertoire in the zoo population. Four of ten putative innovations recognized in the field and potentially present in captivity did not occur despite appropriate conditions, suggesting they are indeed innovations. Second, we experimentally produced relevant conditions to evaluate whether another five potential innovations could be elicited. Based on their continued absence or on their latencies relative to known behaviors, four of the potential innovations could be assessed as innovations and one as a modification. Because 53% of relevant innovations recognized in the field could be confirmed in this analysis, and another 27% assigned possible innovation status, we conclude that the geographic method for detecting innovation in the wild is valid. However, the experiments also yielded up to 13 additional innovations, suggesting that zoo orangutans are far more innovative than wild ones. We discuss the implications of this latter finding with regard to limiting factors for the expansion of cultural repertoires in wild orangutans.

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Introduction

Animal cultures and traditions (Fragaszy and Perry 2003) refer to learned behaviors that are maintained in a population through socially mediated learning. Ever since the first reports of animal traditions appeared (Kawai 1965), great effort has been made to understand the social learning processes that underlie their diffusion and maintenance (Heyes and Galef 1996; Box and Gibson 1999; Galef and Giraldeau 2001; Laland 2004; Whiten et al. 2004; Caldwell and Whiten 2006). In contrast, although innovation is a key component of most definitions of culture (McGrew 1998; Rendell and Whitehead 2001) and the ultimate source of all cultural change (Kummer 1971; de Waal 2001), it was largely ignored until Reader and Laland's (2003) edited volume recently rekindled interest in it (Reader and Laland 2002; Day et al. 2003; Lefebvre et al. 2004; Kendal et al. 2005; Sol et al. 2005; Bouchard et al. 2007; Whiten and van Schaik 2007; Boogert et al. 2008).

This neglect of innovation can be explained at least partly by conceptual difficulties. First, innovation is always relative to some standard. The most commonly used definitions (Kummer and Goodall 1985; Reader and Laland 2003) regard an innovation as a learned behavior pattern that was not previously present in the population. However, this inevitably means that what is considered an innovation depends on the size of the population and the duration of the study. Thus, one can recognize a gradient from weak to strong innovation to invention (cf. Ramsey et al. 2007), although there are no objective criteria enabling demarcation of discrete regions on this gradient. Experimentally, the degree of innovativeness can be operationalized by estimating the average latency among a set of individuals until the first occurrence of the innovative behavior under the appropriate conditions, but this criterion cannot be applied under field conditions. Second, a related problem is that of delineation: when is a behavioral action a new innovation rather than a slight variation or modification of a routine action or an existing innovation? Ramsey et al. (2007) suggested various criteria, dependent on the extent to which their functional use by individuals is different, but in practice there may often be insufficient data to apply these criteria. Third, and most pressing, is the problem of operationally recognizing innovation. It is rarely practicable to use the first occurrence in a population as the operational criterion, because this requires very long-term study (but see Nishida et al. 2009). An approach that may be more feasible for use in natural populations is to focus on specific characteristics of the innovative behaviors, for example an incomplete geographic distribution or low prevalence within a population.

These considerations led Ramsey et al. (2007) to suggest a new approach to assessing innovations in nature. Basically, an innovation is a behavior shown in some populations or individuals, but not in others, where its absence is because of a lack of knowledge rather than different physical or social conditions or different genetic backgrounds. More precisely they set up three criteria for innovations. First, an innovation is a non-universal behavior, i.e. it is either present in some populations and absent in others, or it is present in all populations but then only shown by a few individuals. Their second criterion concerns the properties and the contexts of the behavior: an innovation must not reflect a particular status of the individual (e.g. age class, reproductive state, social position), because a behavioral pattern might be rare overall, but quite frequent among individuals of a particular status, such as infanticidal behavior of males having taken over a group. A behavior must also not be rare because the context in which it occurs arises only rarely. The third criterion, following Reader and Laland (2003), requires that the behavior be performed at least twice to qualify as an innovation, in order to distinguish innovations from accidental behavior. Ramsey et al. (2007) suggested that this procedure allows us to identify innovations.

Applying the approach of Ramsey et al. (2007), van Schaik et al. (2006) compared the data collected in an intensive field study of Bornean orangutans (*Pongo pygmaeus*) with results reported for six other sites, four on Bornean orangutans and two on Sumatran orangutans (*Pongo abelii*). Using this procedure they generated a list of 43 potential innovations in orangutans, henceforth referred to as the *preliminary list*. However, as both Ramsey et al. (2007) and van Schaik et al. (2006) emphasized, this result needs to be validated, because some of the absences of behaviors could be artificial (rather than due to ignorance on the part of the animals), because observers in one place could have failed to recognize particular behaviors or because the conditions under which they can be performed arise only rarely. This uncertainty can by reduced by comparison with an additional population, where conditions are appropriate for investigated behaviors to occur spontaneously and observers could not miss it, or where we can create the required conditions experimentally, which can best be done in captivity.

The objective of this study, therefore, was to validate the geographic method for recognizing innovations, using a captive population to test the preliminary list in two ways. First, the captive population adds another population to the comparison, which is likely to be independent of the others investigated in the field so far. Because the founders of the zoo population were almost certainly captured as infants, even if they hailed from a population where some of these 43 innovations were later observed, the chances they could have already learned any of them are negligible. Thus, the zoo population qualifies to a large extent as an independent new data point. We therefore attempted to validate the innovation status of the putative innovations from the preliminary list by examining which of those that were potentially observable in the zoo population occurred spontaneously. This comparison would indicate that behavior patterns that are on the list but absent in the zoo population are innovations.

Second, and more importantly, we can perform experiments to reveal whether the absence of a particular putative innovation is because of actual lack of knowledge of how to perform it or, instead, because of unsuitable physical or social conditions. We therefore selected those potential innovations from the preliminary list for which we could feasibly create the required physical conditions in captivity needed for their occurrence. We then recorded which of those behaviors actually occurred under these conditions and if so, after which latencies, investigating their innovation status by considering the following three possible outcomes. First, all or most animals would immediately respond to the new condition and stimuli by performing the particular behavior from the preliminary list (or any other behavior from that list). In that case, this behavior would not represent an innovation, but rather a common response to the new condition, and its absence in some populations in the wild is likely to be because of the absence of the proper eliciting conditions, or perhaps recording error. For example, Morand-Ferron et al. (2004) could easily elicit dunking of food pieces in an experiment with wild-caught Carib grackles, *Quiscalus lugubris*, despite its absence in field observations, by offering different social conditions.

Second, the behavior could not be elicited within a reasonable period of time. This suggests that it is not part of the zoo population's behavioral repertoire and thus an innovation in the wild. (We assume that a lack of time to invent it cannot account for its absences in some wild populations.) Third, following a period of clear orientation and attention to the condition or stimuli, the putative innovation would be shown after some time by a first animal and subsequently be shown repeatedly by that individual. In this third case, the behavior would also qualify as an innovation, because it is not part of the individual's spontaneous behavioral repertoire. The behavior obviously remains an innovation if it is later learned by other group-members through individual or social learning.

Behaviors belonging to individuals' spontaneous repertoire are therefore likely to be distinguishable from innovative responses because of their different latencies of first occurrence. Within the same context (e.g. a specific experiment) we expect these latencies to be shorter for known behaviors than for innovative behaviors, assuming we can demonstrate that the latency between exposure to the relevant stimuli and the first occurrence of the behavior is not because of lack of interest on the part of the animals. Furthermore, the longer this latency across individuals, the higher the degree of innovativeness we ascribe to the behavior in question.

Methods

Animals and living conditions

The study was conducted in Zurich Zoo. Subjects were neither food nor water-deprived. The zoo population consisted of Sumatran orangutans, 7 females (ages: Lea 40; Timor 32; Selatan 24; Oceh 19; Tuah 14; Xirah 10; Cahaya 5) and 2 males (ages: Djarius 13; Dahulu 4 (excluded from experiments because of young age)). They were socially housed in one main indoor cage (480 m^3), an adjacent smaller indoor cage (192 m^3), and an outdoor cage (188 m^3). In addition, they had the opportunity to retreat into boxes formerly used as sleeping boxes, out of sight of visitors. The cages were equipped with tree trunks and ropes, which allowed the animals to show their natural locomotion, and a water source; an environmental enrichment program was provided almost daily.

Directly observable behaviors

Baseline data were taken to assess the population's behavioral repertoire, but also to record which of the potentially observable behaviors from the preliminary list compiled by van Schaik et al. (2006) occurred spontaneously in our captive population (Table 1). Behaviors recorded were those from the preliminary list, and any others compiled for

Table 1 Potentially directly observable behaviors from the preliminary list, i.e. all behaviors from the preliminary list that could occur spontaneously in the zoo, given the captive conditions

Behavior[a]	Zoo *N*	Tuanan	*N* wild pops	Conclusion
Auto-erotic tool (c10)	0	A	2/7	I
Scratch with stick (c9)	0	R	3/7	I
Twig biting (c13)	0	H	1/3	I
Branch dragging (i9)	0	A	1/6	I
Branch cushion (c27)	3	H	1/3	pI
Symmetric scratch (c12)	2	A	2/7	pI
Leaf gloves (c16)	2	E	2/5	pI
Tree-hole tool-use (c17)	8	A	1/7	I?
Female rubbing genitals together (i1)	1	R	4/7	N
Autoplay with water (i17)	1	R	1/1	acc

[a] Numbers in parentheses correspond to the numbering of van Schaik et al. (2006)

The column "Zoo *N*" states how many of our nine subjects in Zurich Zoo have shown a certain behavior

In column "Tuanan" we present the cultural status of the same behaviors at Tuanan (van Schaik et al. 2006), categorized as follows: A, absent; R, rare; H, habitual (several individuals); C, customary (most individuals); E, absent for ecological reason

The column "*N* wild pops" states the number of wild populations where the behavior has been found (van Schaik et al. 2006), out of the number of populations where (i) ecological conditions allowed for the behavior to be shown and where (ii) its absence or presence is reported

The column "Conclusion" briefly explains which conclusion we draw for each candidate behavior concerning its innovation status: I, behavior was absent in the zoo population and therefore is an innovation in nature; pI, behavior was rarely shown by a few individuals, not depending on an individual's particular status, thus is a possible innovation; I?, unclear if this is an earlier innovation that spread successfully; N, behavior was regularly shown, but only by individual(s) of a particular status, thus it is not an innovation; acc, behavior occurred only once, maybe accidentally, thus not qualifying as an innovation the field study but not found to be innovations, the orangutan ethogram (Rijksen 1978; see also http://www.aim.uzh.ch/orangutannetwork.html), and any other noteworthy behaviors (involving unusual actions or action–object combinations). In total, 95 h of baseline observations were made in the indoor cages of the orangutans from the zoo's visitor room, with observations made between 10 a.m. and 5 p.m. during nearly 3 months. At the time, the orangutans were only rarely outside, and the outside cage did not contain physical elements not found in the indoor cages. Baseline data were collected as 1-h focal samples, systematically alternating between subjects to ensure equal coverage of all individuals. At the same time, additional data were recorded by ad libitum sampling (Altmann 1974), in order to record rarely appearing behaviors that otherwise would have been missed. Because no sounds of the orangutans were audible in the visitor's room where the baseline observations were made, the behavioral repertoire recorded does not include vocalizations.

In order to assess the completeness of the behavioral repertoire of the population, and thus also the extent to which we sampled the directly observable behaviors from the preliminary list from the wild, a cumulative record of first appearances (a so-called collector's curve) was constructed (Tomasello and Stahl 2004). To estimate the repertoire size of the group, we fitted an arctangent function to the cumulative number of first appearances of behaviors per observation hour. This was done by repeatedly applying tangent-transformations with different asymptotes to the data in order to linearize it, and then fitting a line with least-squares regression (DMK 2006). The linearization with the best fit (highest R^2) was then selected. The function of the corresponding tangent transformation yields the value of the asymptote of the original, untransformed data, and this asymptote represents the estimated size of the group's behavioral repertoire.

Furthermore, we wanted to compare the behavioral repertoire of our zoo population with that of a wild one. We therefore also constructed a corresponding collector's curve for the wild population of orangutans from Tuanan (Borneo), using the same criteria as above. These data were solely based on focal animal sampling, whereas in the zoo we also relied on additional ad libitum sampling. However, because the zoo records were almost certainly largely complete, we decided to make the collectors' curves of the zoo and the wild population comparable by assuming we conducted 9 parallel focal samples in the zoo. Although some behaviors may have been missed, the resulting underestimation of the zoo curve is conservative because the zoo curve rises more steeply than the wild curve. This procedure allowed us to compare after how many observation hours 95% of the behavioral repertoire had been observed in zoo and wild population.

Experimental elicitation of behaviors

For the experimental part we selected those behaviors from the preliminary list for which we could feasibly provide the required conditions in captivity, giving the animals the opportunity to show them. Experiments were carried out at the group's main indoor cage, where subjects could put their forearms through the grid and sounds were audible. Because we tested subjects as a group, only the first individual to show a certain new behavior would be considered its innovator. Briefly, with a blow-pipe experiment, we attempted to elicit kiss-squeaks on leaves. Further experiments involved smearing hot sauce to make "Leaf-body scrub" and "Leaf napkin" possible; and offering syrup in a vertical tube to elicit "Branch scoop" and "Sponging". These behaviors are listed below, along with their definition and a description of the corresponding experiment we performed:

- "Kiss squeak with leaves": Using leaves on mouth to amplify sound. They are performed towards other orangutans, human observers, or predators to intimidate or scare them away.

Blow-pipe experiment: We simulated a dangerous condition by introducing a person with a blow-pipe who occasionally aimed with the blow-pipe at the animals for 7 min. The animals were familiar with the blow-pipe in connection with medical treatment by a veterinarian and they were known to respond strongly with distress signals. But on those previous occasions no leaves had been available, whereas under these experimental conditions leaves were now provided. Data were gathered continuously by behavior sampling.

- "Leaf body scrub": Using a leaf to clean body surface (remove dirt from the fur). In captivity, instead of leaves, wood wool or paper could also be used.

Smearing experiment: In three sessions of approximately 30 min on different days a zoo keeper smeared hot sauce (a mixture of Tabasco and Sambal Oelek) with a long brush on their body. Ideally, each individual was targeted at least once in a session; however, this was not always possible. Data were collected continuously by behavior sampling.

- "Leaf napkin": Using handful of leaves to wipe latex off the chin after eating fruit. This behavior was also investigated in the "Smearing experiment", but hot sauce was smeared under the subjects' chins instead.
- "Branch scoop": Drinking water from deep tree hole using a leafy branch.

Syrup tube experiment: In seven sessions of 90 min on different days, two transparent tubes that were approximately one quarter full with syrup were fixed to the outside of the cage. Animals were able to reach with their arms through the grid of the cage. The tube used was 35 cm in height and 10 cm in inner diameter, which allowed the orangutans to reach about 20 cm inside the tube with their hands (except for the male adult, who could not reach inside the tube). Sticks, twigs (with leaves), wood wool, and paper were provided. Separate video cameras were directed at each tube and recording was performed continuously. Continuous behavior sampling was from video tapes. At the same time this experiment was run to provide the proper conditions for "Sponging" to be possible.

- "Sponging": Using crumpled leaves to absorb water from a tree hole, then drink the water from the leaves.

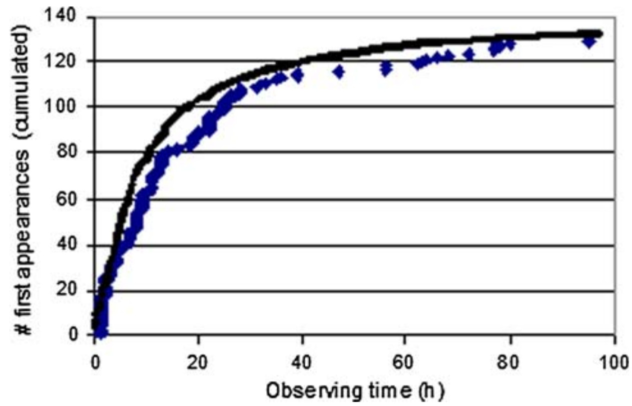

Fig. 1 Cumulative collector's curve: The cumulated number (*freq.*) of first appearances of behaviors per observation hour by focal subjects ($N = 9$). The *continuous line* represents the function $y = (282/\pi) \times \arctan(x)$, with an asymptote value of 141 yielding the best fit to the data

Results

Assessing the completeness of the behavioral repertoire

During 95 h of baseline observations, 129 distinct behavior patterns were recorded using focal sampling, and an additional nine by use of ad libitum sampling, for a total of 138 (Appendix 1). Figure 1 shows the cumulative number of recorded behaviors obtained through focal sampling as a function of observation time (a so-called collector's curve), and the best fitting function. After 68 h of observation, 95% (123) of all observed behaviors had been recorded, which means that in the following 27 h of observation, only 6 more behaviors were performed for the first time. The function that best fitted our data (Fig. 1) $y = (282/\pi) \times \arctan(x)$ yielded an expected repertoire size of 141 behaviors (asymptote, $R^2 = 0.983$), only marginally exceeding the observed 138. Thus, our record of the local behavioral repertoire was largely complete, and we can be confident that behaviors that had not been recorded were not part of the population's behavioral repertoire at the time. It was therefore valid to compare our sample with that from the wild populations and to assign behaviors from the preliminary list that could potentially be directly observable in captivity but that did not occur within our observation time as innovations.

Comparison of our captive population with natural populations: directly observable behaviors

Table 1 furnishes a detailed overview of the assessments of the innovation status of all ten behaviors. Six out of ten behaviors from the preliminary list that were potentially directly observable (Table 1) occurred spontaneously in our captive population. Thus, the remaining four that did not occur were not part of the captive population's behavioral repertoire and could therefore be validated as innovations. Those six that did occur would still represent innovations if they had originated as an individual's innovation that subsequently spread through our zoo population (in which case comparisons with other captive populations would show that they are missing in other captive populations). Here we have the same problem as field workers, and in order to be conservative, none of the behaviors on the preliminary list that had been observed were considered innovations until further investigation suggested otherwise.

The first three of the following six behaviors that did occur could possibly be earlier innovations, because they were rare and apparently did not depend on a particular status of the individuals showing them:

1. "Symmetric scratch" was shown by two different animals once each (Ti 1x, Tu 1x), despite abundant opportunities;
2. "Branch cushion" was shown at a slightly higher individual rate by three of nine individuals (Sel 3x, Dj 2x, Tu 1x); and
3. "Leaf gloves" was shown by only two individuals, although all subjects had been handling nettles to eat them.

"Tree-hole tool use" was shown by 8 of 9 subjects, but is rare in the wild (Table 1), leaving us in this case with an unclear innovation status. Another behavior (females rubbing genitals together) was regularly performed by one 5-year-old female Cahaya (6x), and thus more likely to be an example of status-dependency and not an innovation. "Autoplay with water" was shown only once (by Ca) and might be accidental or state-dependent.

To summarize, four of the ten behaviors classified as innovations through the geographic approach were assessed as innovations by our zoo study. Moreover, three of the remaining six are possible innovations, but the remaining ones are probably not.

Comparison of captive and natural populations: experimental elicitation of behaviors

In the experimental part, we selected those five behaviors from the preliminary list that could potentially be elicited in captivity through offering appropriate conditions. Four could be classified as innovations, one as a modification, as shown below.

The "Blow-pipe" experiment was aimed at eliciting "Kiss squeaks on leaves", but only ordinary kiss squeaks were performed, and not the *kiss squeak on leaves*, despite the availability of leaves. Thus, the latter was assessed as an innovation. In the other experiments, the remaining four appropriate behaviors were indeed elicited (Table 2). This result might suggest that most putative innovations described in the field were not in fact innovations, but the pattern in the latencies suggests otherwise, as elaborated below.

In addition to behaviors on the preliminary list, however, several others accrued, resulting in a total of 13 potential innovations that occurred during experimentation, nine alone in the "Syrup tube" experiment. All these potential innovations are listed and described in Table 3, along with the identity of the innovator and the latency from the beginning of an experiment until the novel behavior occurred. Only five of 13 were shown more than 1 h after the conditions had been offered, the slowest after 10 h. Most occurred within 1 h (often being performed by more than one subject), suggesting that they do not qualify as innovations, following the criteria of Ramsey et al. (2007).

Table 2 Experimental elicitation of behaviors: lists those behaviors from the preliminary list we tried to elicit experimentally in captivity through offering the required conditions

Behavior	Zoo *N*	Tuanan	*N* wild pops	Conclusion
Kiss-squeak with leaves (c2)	0	C	3/7	I
Leaf body scrub (i2)	6	A	1/7	I (lat)[a]
Leaf napkin (c14)	6	A	1/7	I (lat)
Branch scoop (c19)	4	A	1/7	I (lat)
Sponging (i11)	5	A	1/7	I (lat)

One animal was not considered for experiments (Dahulu). Otherwise the same explanations as provided in Table 1 apply

The column "Conclusion" consists of an additional explanation: I (lat) behavior qualifies as an innovation on the basis of the relative latencies of behaviors occurring within this experiment

[a] Modifications of previous innovations

In order to determine whether these behaviors of the experiments "Syrup tube" and "Smearing" were part of the population's repertoire, or whether they were invented during experimentation and thus represented innovations, we analyzed their latencies in more detail across individuals. Complete information about the latencies after which subjects successfully performed a particular behavior for the first time can be found in Appendix 2. Because we do not expect an absolute threshold for latency to indicate innovations, we examined the relative latencies of behaviors within each experiment separately. For the experiments "Syrup tube" and "Smearing" we analyzed the latencies after which subjects used distinct techniques for the first time. Lea was excluded from the "Syrup tube" experiment, because she never manipulated the syrup tubes. A Friedman Test revealed that techniques of the "Syrup tube" experiment varied highly significantly in the latency until first performance among the seven individuals (Friedman test: $\chi^2 = 17.294$, $N = 7$, $k = 6$, $p = 0.004$; techniques where the same behavior was applied to different materials were combined for this analysis). A follow-up procedure (Sachs 1999), in which a sum of ranks difference threshold between two behaviors is calculated, showed that significant differences only arose between a pair of techniques if one of them was "Dip stick". The behavior "Dip stick" differed from the rest in latency of occurrence in being shown by several individuals within much shorter latencies than the other techniques, as illustrated by Fig. 2a. "Dip stick" is thus an example of a behavior that was already part of the population's repertoire, a suggestion confirmed by observations of tool use with sticks applied to environmental enrichment tasks during the baseline period.

All the other eight techniques used in the experiment "Syrup tube" were not shown by most individuals after such a short latency, suggesting that they were indeed invented during the experiment, representing anything between strong innovations, weak innovations, or modifications. As stated earlier, the average latency across individuals until the first occurrence of (innovative) behaviors in the appropriate conditions may be the best way to operationalize the degree of innovativeness. Thus, a rather low average latency as in "Branch scoop" would suggest a weaker innovation, as opposed to the high latency of "Twisted paper rod" indicating a stronger innovation (Fig. 2a).

There are three reasons to assign these behaviors at least some innovation status. First, individuals were engaged with the apparatus before finding a first alternative solution to "Dip stick". Thus, we can exclude that animals simply have been inactive in the meantime and therefore all other solutions were not invented either but simply remembered later (although this argument should

Table 3 Description of the potential innovations and their modifications that occurred during experiments, stating the respective innovator, and the latency (hh:mm:ss) from the beginning of an experiment until the innovation occurred, sorted by experiment and latency

	Behavior	Experiment	Description	Innovator	Latency
1	Leaf napkin	Smearing	Using a leaf, wood wool, or paper to wipe the sauce off the chin	Tu	00:01:02
2	Leaf body scrub[a]	Smearing	Using a leaf, wood wool, or paper to wipe the sauce off the body surface	Dj	00:14:30
3	Shield	Smearing	Using a respectable amount of paper or wood wool in front of the body as a protection shield to prevent being smeared	Tu	00:20:50
4	Rub off	Smearing	Clean the sauce off self by rubbing it off on the ground or a tree	Dj	00:32:25
5	Clean somebody with napkin	Smearing	Clean the sauce off somebody by wiping it off with a napkin (i.e. leaf, wood wool, or paper)	Ca	01:08:00
6	Fish	Syrup tube	Fishing in the tube with a stick to retrieve leaves, paper, or wood wool that have accumulated in the tube as a result of the previous action of subjects	Tu	00:11:17
7	Branch scoop	Syrup tube	Use a twig with leaves like a rod, so hand is only slightly or not at all inside the tube; pull twig out, then suck syrup out by gently chewing the leaves	Sel	00:12:30
8	Paper squash	Syrup tube	Force paper directly with hand into the tube, pull paper out, take it in mouth and suck it	Tu	00:39:15
9	Wood wool squash[a]	Syrup tube	Push wood wool down into the syrup, pull it out, take it in mouth and suck it	Ti	00:40:15
10	Sponging	Syrup tube	Paper or wood wool chewed to a ball is dropped inside the tube; then reach with hand down into the syrup, take it out by hand, take the whole piece into the mouth, chew and suck it (like chewing gum)	Ca	01:44:00
11	Vegetable rod[a]	Syrup tube	Using vegetables like leek or chard as a rod by holding it down into the syrup, taking it out and sucking it	Sel	02:46:00
12	Twig squash[a]	Syrup tube	Squash twig into the tube with hand reaching inside the tube, then pull it out and suck it	Tu	04:33:00
13	Twisted paper rod (TPR)	Syrup tube	Twist paper and use it as a rod by holding one end down in the syrup, pulling it out, and sucking it	Sel	09:59:00

Omitted are "Dip stick" (dip a bare stick into the tube, then lick the syrup from the tube; latency: 00:00:50) and "Clean with hand" (wipe off sauce with hand; latency: 00:00:05), which also occurred during experiments, because they were not considered innovations

[a] Modifications of previous innovations

equally apply to "Dip stick"). We measured subjects' active engagement by means of the frequency of 1-min intervals they were either observing the apparatus or an individual manipulating it from close distance (less than 20 cm), or touching the tube with their hands, manipulating it unsuccessfully, or using the technique "Dip stick". Indeed, as Fig. 2b illustrates, subjects were much more engaged with the task before showing a first alternative solution to "Dip stick" compared with before applying "Dip stick" for the first time (Wilcoxon signed-ranks test: $Z = -2.032$, $N = 5$, $p = 0.042$). Therefore, we conclude that the behavior "Dip stick" was already in the population's repertoire, whereas the other eight solutions were invented during the experiment (including the two behaviors from the preliminary list: "Branch scoop" and "Sponging"), and therefore represent innovations.

The second argument is that longer latencies until first occurrence do not simply indicate that these are non-preferred techniques already known to the animals. Thus, after its first occurrence an innovative behavior was performed more often (within shorter time), which would not make sense if they were non-preferred, known behaviors. We analyzed the time intervals until first occurrence of an innovative technique and between the seven subsequent occurrences in the experiment "syrup tube". A Friedman test showed that these time intervals were significantly different (Friedman test: $\chi^2 = 17.537$, $N = 8$, $k = 8$, $p = 0.014$). The same follow-up procedure described above (Sachs 1999) showed that significant differences only arose between two time intervals if one of the two was the time lag until the first performance of a behavior. This first time interval differs from the following seven, which

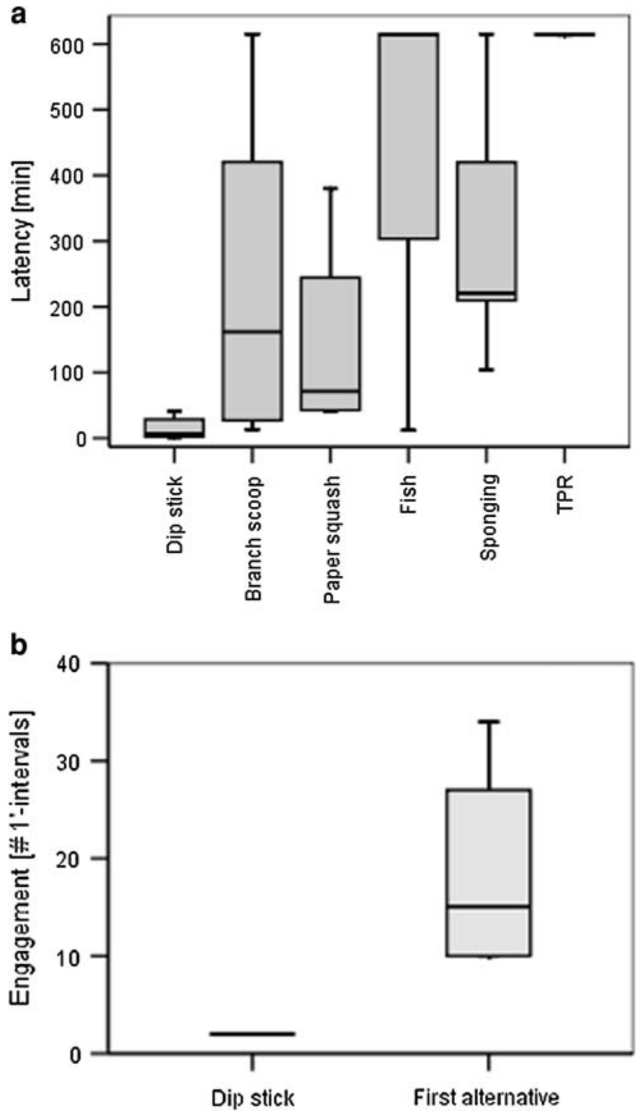

Fig. 2 **a** Latencies (min) until individuals' ($N = 7$) first successful performance of a technique in the experiment "Syrup tube". For individuals that never showed a particular behavior, the latency was set coinciding to the duration of the experiment (615 min). Medians and quartiles are shown. **b** Frequency of 1-min intervals in which individuals ($N = 5$) were actively engaged with the task, before showing the technique "Dip stick" for the first time, and before a first solution other than "Dip stick". Medians and quartiles are shown

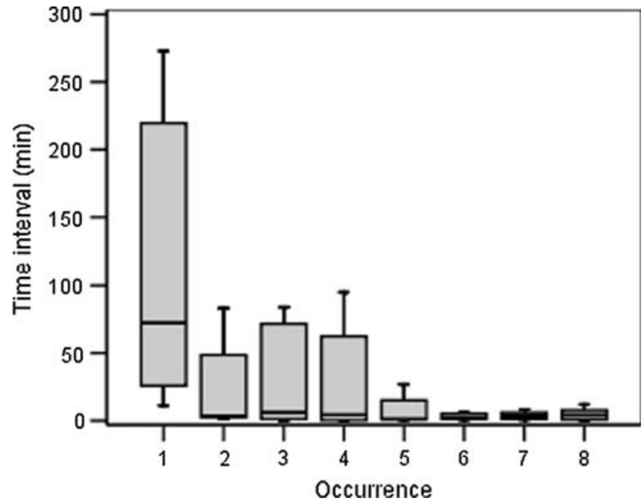

Fig. 3 Time intervals (min) until first occurrence of behaviors ($N = 8$) and between the seven following occurrences in the experiment "Syrup tube". The time lag until the first performance of behaviors (occurrence 1) is higher than between the other occurrences. Medians and quartiles are shown

were all shorter, as illustrated in Fig. 3. Page's L trend test (Page 1963) was used to test for a successive decrease of these eight time intervals. It revealed that there is a highly significant trend for time intervals to become shorter (Page's L trend test: $L = 1452$; $k = 8$; $N = 8$; $p < 0.001$). Therefore, we can also exclude the possibility that these behaviors had been non-preferred, known techniques.

The third argument is that even apparently similar techniques seem to be functionally different from the orangutan's perspective. Where the same behavior pattern is applied to a different material, but animals do not use the materials randomly and interchangeably, we regard them as modifications of an innovation (Table 3). In the case of "Wood wool squash", "Paper squash", and "Twig squash" the same behavior pattern is applied to different materials. However, our subjects discriminated between these three forms. Although these materials were all continuously available, only two of six animals using any of the three materials used all of them; two animals used two of the three materials, and two animals used only a single material (Appendix 2). Furthermore different subjects preferred different materials: three animals preferred wood wool to paper (19 vs. 5 min; 1 h 27 min vs. 36 min; 11 vs. 2 min), whereas another animal used paper twice as often as wood wool (1 h 13 min as opposed to 38 min), and only one animal used paper and wood wool equally much (9 min; 8 min), while both materials were always equally abundant. Thus, animals clearly distinguished between the three techniques. Therefore, "Wood wool squash" and "Twig squash" are assessed as modifications of the innovation "Paper squash", as the last occurred first. On the other hand, the behavior pattern of "Sponging", where paper is chewed to a ball and then dropped, is clearly different from "Paper squash", where a large amount of paper is directly forced into the tube. Finally, "Branch scoop" is a different behavior pattern from "Dip stick" (gently sucking syrup out of leaves as opposed to licking it from a bare stick), whereas "Vegetable rod" is a modification of "Branch scoop", and "Twisted paper rod" is, again, a different behavior from "Vegetable rod".

For the "Smearing" experiment, a Friedman Test revealed that the techniques also had highly significantly different latencies until first performance among the eight

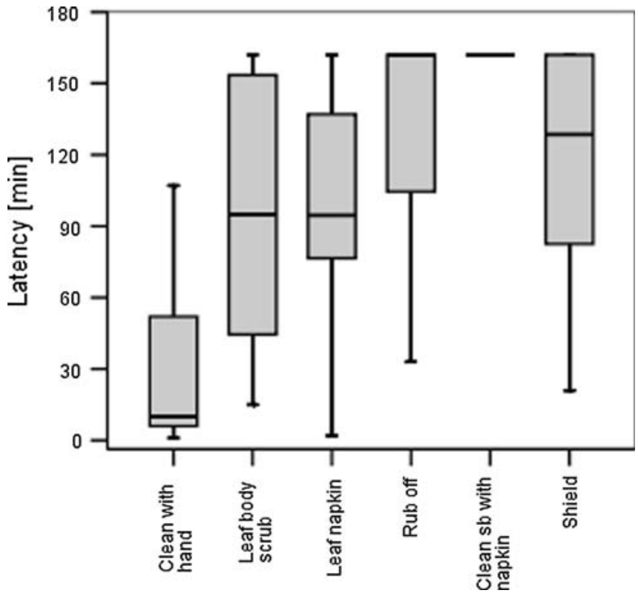

Fig. 4 Latencies (min) until individuals' ($N = 8$) first successful performance of a technique in the experiment "Smearing". For individuals that never showed a particular behavior, the latency was set coinciding to the duration of the experiment (162 min). Medians and quartiles are shown

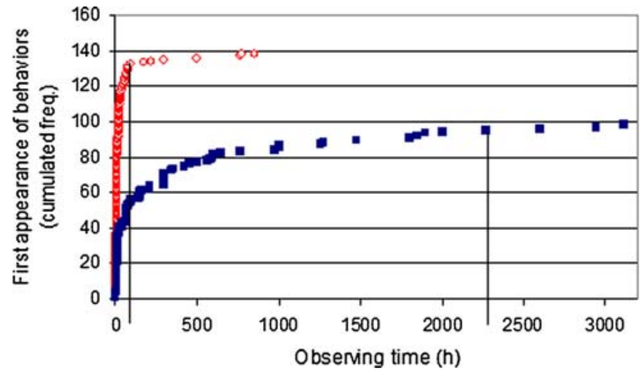

Fig. 5 Cumulative number of behavior patterns as a function of observation time (collector's curve) for wild (*full squares*) and zoo (*open circles*) orangutans. To make them comparable, the zoo data were treated as 9 parallel focal samples (because the additional ad libitum sampling was considered nearly complete). Vertical lines indicate the time at which animals in the wild or the zoo reached 95% of their repertoire

individuals (Friedman test: $\chi^2 = 17.602$, $N = 8$, $k = 6$, $p = 0.003$). The follow-up procedure (Sachs 1999) showed that significant differences between two techniques were found only if one of the two was "Cleaning with hand". This simple cleaning with the hand differed from the other techniques in latency of occurrence, as several individuals showed it sooner than the other techniques, as illustrated in Fig. 4. We thus conclude that whereas "Cleaning with the hand" was already part of the subjects' repertoires, the other five techniques (Table 3) were invented during the "Smearing" experiment and qualify as innovations, including the two behaviors from the preliminary list ("Leaf body scrub" and "Leaf napkin") that inspired the experiment. The latter are very similar, but subjects apparently made a distinction: four animals showed both of them, but another four animals only showed either one or the other (Appendix 2). "Leaf body scrub" is therefore regarded as a modification of the earlier occurring "Leaf napkin". Subjects clearly disliked being smeared, as indicated by their attempts to avoid it and their facial expression when they had been hit; therefore there was no need to quantify their motivation for solving this task.

Comparison of the corresponding behaviors with those of a natural population (Tuanan)

Comparison of collector's curves of captive and wild populations (Fig. 5) showed that the captive population had a larger behavioral repertoire. Moreover, zoo subjects showed their full repertoire within a much shorter time than the wild population, suggesting that they showed the elements in their repertoire more frequently. Within 80 h of observation time zoo animals showed 95% of their behavioral repertoire, whereas the wild ones took over 2,000 h to show the corresponding proportion. Although the habitats are not directly comparable, these differences suggest a larger innovation repertoire in the zoo, i.e. that zoo animals were more innovative, and that each element is shown more frequently.

Discussion

The validity of the geographic method

We found that of the ten potential innovations from the wild (van Schaik et al. 2006) we could potentially expect to observe directly in zoo conditions, four did not occur in the zoo, even though we could be confident we had collected an adequate sample of the zoo population's repertoire. These four were therefore considered innovations. Of the other six, three may be possible innovations, because they were rare and, apparently, did not depend on the particular status of individuals showing them (Table 1).

The experiments allowed us to qualify this conclusion. Of the five behaviors from the preliminary list that we could potentially elicit in captivity by experimentally offering the relevant conditions, only one did not did emerge (Table 2). "Kiss squeaks with leaves" was not performed in the "Blow-pipe" experiment. Although this experiment was very short and conducted only once in order to minimize stress, it successfully established the appropriate conditions, as subjects did respond with regular kiss squeaks. “Kiss squeak with leaves” is thus neither part of our subjects’ behavioral repertoire, nor was it invented during the experiment; its occurrence in the wild can therefore be classified as an innovation.

Although those that were actually elicited in the experiments might seem unlikely to be innovations or modifications, they nonetheless were. Based on latencies across individuals we confirmed the innovation status of “Branch scoop”, “Sponging” and “Leaf napkin”, whereas “Leaf body scrub” was assessed as a modification. This was possible because in the experiments several other behaviors also occurred, allowing us to distinguish between solutions that were already part of the population’s repertoire and techniques that were invented during the experiment. Latencies of “Dip stick” in the “Syrup tube” experiment and simple cleaning with bare hand in the “Smearing” experiment were significantly shorter relative to latencies of other techniques in the specific experiments; this suggests that the former were already in the population’s repertoire, whereas the latter were invented during the experiments. Subjects were not inactive in the meantime but in fact clearly engaged with the syrup tube before showing a first alternative solution to “Dip stick.” Furthermore we could rule out the possibility that the longer latencies of techniques other than “Dip stick” in the experiment “Syrup tube” indicated non-preferred, known behaviors, rather than innovations. We demonstrated that time intervals between consecutive occurrences of innovative behaviors were significantly smaller after the first occurrences, which would not have been found if these had simply been non-preferred but known techniques. There is no explanation for why time intervals between two subsequent occurrences of non-preferred techniques should decrease; but it makes good sense in case of innovations that are more frequently performed by the inventor after their initial occurrence, and eventually also by some groupmembers having learned the new technique either socially or on their own. Finally we showed that orangutans discriminate among similar techniques, which were therefore distinguished as modifications.

In conclusion, our attempt to validate the geographic approach for identifying innovations in wild populations by comparison with a captive population suggested that at least eight of the 15 investigated behaviors from the preliminary list (putative innovations recorded for wild orangutans) could indeed be classified as innovations, and one additional behavior as a modification (Tables 1, 2). First, at least four of the ten behaviors from the preliminary list we could expect to observe directly were verified innovations in our captive population based on their absence (Table 1). Second, attempts to experimentally elicit five additional behaviors from the preliminary list showed that four qualified as innovations and one as modification, based in one case on absence and in the remaining others on latencies of first occurrence across individuals (Table 2). Thus, in total at least 53% (8 of 15) of the putative innovations recorded for wild orangutans were assessed as innovations. If we add the three possible innovations and the modification (Table 1), this figure becomes 80%. Therefore, our findings largely confirm the assessments on the preliminary list by van Schaik et al. (2006) and thus the approach of Ramsey et al. (2007).

The geographic method largely relies on patterns of presence and absence to assess a behavior’s innovation status, making it difficult to assess its degree of innovativeness. The experimental approach, by measuring latencies, allows for a quantification of the strength of the innovations hitherto unavailable. Future work could use this quantification to test hypotheses about the different strengths of innovations.

Innovativeness in the zoo and in the wild

The data also revealed a phenomenon that was not part of the original objective of this study. The zoo environment seems to be conducive for the emergence of innovations. Several observations support this conclusion. First, the repertoire comparison (Fig. 5) suggests a far larger innovation repertoire in the zoo population. Although temporal variability in habituation, ecological conditions and climate and poorer visibility in the wild may play a role in this difference, the recent origin of the zoo population compared with the wild ones would have suggested a much smaller repertoire in zoos. Second, the appropriate experimental conditions elicited many more innovative responses in captivity than had been observed in the wild, and moreover, did so in a remarkably short time frame. In the “Syrup tube” experiment alone, which represented an imitation of a tree hole filled with water, the subjects of a single zoo population came up with five innovative solutions and three modifications, as opposed to the mere two innovations recorded in a total of seven wild populations. The data suggest the existence of a gradient of innovations, with a rather low average latency as in “Branch scoop”, suggesting a rather weak innovation, and a long latency of “Twisted paper rod” in the same task, indicating a stronger innovation. Third, we also observed several other behaviors in our captive population under regular conditions not reported from the wild. Two of these should be possible in the wild, and were therefore potential innovations:

1. “Bag use”: putting small, loose food items on a piece of paper, grabbing its corners to form a bag, and carrying it somewhere else for eating (in nature big leaves could be used for this); and
2. “Foot in mouth”: climbing while having several digits of one foot in its mouth.

Finally, "Tree-hole tool-use" was frequently shown. Indeed, zoo orangutans commonly use sticks to poke in holes and crevices (Jantschke 1972; p. 196), whereas stick use is strikingly absent in most orangutan populations in the wild (Table 1). Similarly, in one wild chimpanzee community where sticks were occasionally used, animals readily applied sticks in a given task, whereas in a second community that did not use sticks, the animals did not (Gruber et al. 2009). Thus, we may have been overly conservative not to assign innovative status to "Tree-hole tool-use".

All these differences indicate that captive orangutans are far more innovative than wild ones. Russon et al. (2009) similarly found that ex-captive rehabilitants who were released on to an island with natural habitat but continued to be provisioned, developed an innovation repertoire in their natural habitat enclosures that was far richer than that found in natural populations. Kummer and Kurt (1965) found that captive hamadryas baboons had added new social behavior patterns not found in the wild populations studied by them. Although Kummer (1992; 1995) suggested that captivity especially promotes social behaviors, the orangutan findings indicate that technical innovations are also more numerous in captivity compared to the wild.

In the wild, infant orangutans rely heavily on what their mother eats and does, and largely eschew independent exploration of the environment (Jaeggi et al. 2009). Even independent orangutans show remarkably little sampling of potentially novel foods (Zweifel 2008). In a simple but pioneering experiment, Menzel (1968) found that wild Japanese Monkeys, *Macaca fuscata*, ceased coming to a previously frequently visited spot after a set of innocuous toys had been placed there, suggesting that they actively avoided the area because of these unfamiliar objects.

Overall, then, there are enough findings to suggest that wild orangutans may have a very low innovation tendency, whereas being in captivity unblocks the innovation tendencies of individual primates. What causes this contrast? The most likely explanation is that wild primates associate unfamiliar, novel objects with danger (be it through poisoning, lack of vigilance, or simply opportunity costs; Halsey et al. 2006) and thus largely avoid them (cf. Menzel 1968), whereas captive conspecifics associate them with a food reward or other positive reinforcement. As a result, captive individuals are more likely to approach and explore novel objects and to do so more quickly than do wild animals. Kummer's (1995) explanation for social life growing luxuriantly in captivity compared with its reduction under food shortage in the field (Morrison and Menzel 1972) may also apply to our findings. Kummer (1995) explained his findings with a separation of an individual's gratification value and the survival value for its genes. The alienation from the environment experienced by zoo animals provided them with more spare time and spare energy (than their conspecifics ever had in the wild), allowing them to play with their gratification system, as a human does. An animal released from the pressure to survive can choose more freely than a wild animal how much exertion, excitement, novelty or uncertainty it wants to experience. The zoo baboons at that time only had their conspecifics to maximize gratification, resulting in a luxuriant social life. Kummer's (1995) explanation of the emancipated gratification system may also apply to our zoo orangutan population. Released from danger avoidance and the intensive subsistence lifestyle of the natural world, zoo orangutans could overcome neophobia and invest their larger amount of spare time and spare energy in manipulation of novel objects and tasks to maximize gratification. This could then yield the higher (technical) innovativeness in zoo orangutans we observed, compared with wild ones.

Furthermore, captive orangutans recognize a task as such probably faster than their conspecifics in the wild. Using a stick as a tool to gain honey is present in some wild populations, but not in most others (van Schaik et al. 2006). In the latter sites, tree holes filled with honey are less abundant, leaving orangutans with a lower probability of inventing a tool-based solution (Fox et al. 2004). In the case of the "Branch scoop" innovation, the wild innovator first had to stumble upon a tree hole filled with water out of arm's reach, in combination with being motivated to get some water. This latency largely ceases to apply in captivity, where a new opportunity is often immediately recognized as such by subjects.

These two factors together (positive association with novelty and easy recognition of something novel as potentially rewarding) add up to innovations appearing in captivity much faster and, given excellent conditions for social transmission, to be retained better in the population, leading to larger population-specific innovation repertoires. (We do not know whether the mean duration of retention in the population differs between zoos and the wild, but "fashions" are certainly not limited to captive populations: Nishida et al. 2009).

A possible alternative, but not mutually exclusive explanation for the wild-zoo contrast is that the increased innovativeness in captivity is an enculturation effect (Tomasello et al. 1993; Call and Tomasello 1996). However, in this zoo population of orangutans, only one animal (Lea) is human-reared, and she did not contribute any of the experimentally induced innovations (Table 3). Tomasello and Call (2004) later changed the enculturation hypothesis to a weaker socialization hypothesis, saying that "in growing up with humans who control their world totally and who interact with them in ways that other apes do not, apes acquire a different set of social skills than their wild conspecifics for interacting with humans" (p. 214).

However, as we saw, it is not only in the social domain that innovations are increased. Thus, neither enculturation, nor socialization can account for the contrast we found.

Finally, the greater innovativeness of captive orangutans compared with wild ones may be relevant to the main issue of this paper: using the captive population to validate the innovation status of behaviors classified as innovations in the wild. Because of the greater innovativeness of the zoo orangutans, the method we used is actually very conservative: if a behavior that qualified as an innovation in captivity is present in the less innovative wild animals, its assessment as an innovation of the wild conspecifics can hardly be false. At the same time we may not succeed in assessing a behavior as an innovation in captivity despite it actually being one in the wild.

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Appendix 1

See Table 4.

Table 4 Behaviors (138) recorded during observational phase of study and components of the zoo collector's curve in Fig. 5

Behavior	Explanation of behavior
Angel	Lying on its back, moving arms up and down (arms are always in contact with the ground)
Avoid	Actor leaves his place (e.g. nest) because another subject is approaching him but apparently not stopping. If the "avoider" lingers, waits and looks back, it is called "hesitant avoidance"
Awry lips	Animal warps its mouth and makes awry lips
Backdance	Lying on its back and circling
Balance on rope	Walk a few steps bipedally and erect on a rope without hands grasping another rope, grid, or anything else for support
Bared-teeth scream	By animals who were attacked and bitten: Loud, high-pitched, drawn-out hoarse screams, each of which may end with a choking sound. Mouth is wide open with the teeth and gums exposed. Thus, also recognizable only visually
Bark biting	Biting into the bark of a tree, sometimes followed by tearing off long strips of bark and then dropping it immediately
Biting	When biting, the actor closes his jaws abruptly, usually on a victim's hand or foot
Brachiate	Body is hanging, arms are extended, feet are in the air or are only partly supportive, the animal is moving by clinging with one hand alternately to branches/roots (for example)
Branch cushion	Cushion a big branch, a wire-nest, or a rope with wood-wool to sit or lie on it
Brusque charge	Actor suddenly rushes towards his opponent, silently and in a straight line. The head is with-drawn between the shoulders, actor often shows piloerection of shoulder- and upper-arm region, accompanied by "frowning" and "tense-mouth". When catching up with the partner, actor may grasp an extremity and bite. Partner is typically fleeing when seeing the actor rushing towards him
Butt-head	Actor presses its bottom in the face of a partner
Call on someone to groom him/her	Actor calls on someone to groom him/her. Actor sits with ostentation in front of a partner, typically showing him his back
Chew	Actor is chewing on something (typically on a stick, or cardboard) but apparently not for feeding reasons
Climb	Using all 4 extremities to move on branch, rope, or grid, up or down
Climb on someone	Youngster climbing around on another orangutan
Climb with foot in mouth	Actor climbs with some fingers of one foot in the mouth, thus using only 2 or 3 extremities to climb
Clinging	Prolonged embracing or clinging to the partner. Hanging/holding on to the partner, potentially hindering the partner's movement: usually by infants
Cushion ground	Cushion the hard ground with wood-wool to sit or lie on it
Direct smell	Smelling directly at the partner's face or shoulder, may result in nose to nose contact
Dive	Dropping the upper part of the body, head down and arms extended, holding on with feet. Results in an extended upside down hanging position
Dragging	Rather fierce grasping or pulling of a partner and dragging him along for some distance

Table 4 continued

Behavior	Explanation of behavior
Drink bowl hl/nhl	Drink water out of a bowl (a) either humanlike (hl) by tilting the bowl and letting the water pour into the mouth, or (b) by holding the head into the bowl (nhl)
Drink directly	Drink water directly with mouth from the fountain
Drink milk	Drink milk from mum
Drink urine	Drink the urine from someone else that is urinating
Drive away someone	Actor is moving towards another animal, but unlike in "join" the actor is not stopping and the partner is leaving (when the actor is coming within a distance of approx. 0–3 m)
Drop	Drop an object the subject was previously carrying around for some time
Feed	Animal takes in food or is chewing food. Animal may move while feeding
	Several variants of feeding on small loose food (e.g. pellets, kernels, grain) are further distinguished:
	Pick-feeding: Picking grain with fingers from the ground and putting in the mouth
	Grazing: Feeding directly with mouth on the ground, supporting the body with 1 or 2 arms or both hands that remain in contact with the ground, or supporting the body by clasping a rope with one hand
	Hand-feeding: Feeding on grain directly with mouth from a heap in the hand
	Box-feeding: Feeding on grain directly with mouth from a heap in a box/paper bag
	Box-pick-feeding: Picking grain with fingers out of a heap in a box
Fill bowl	Fill water in a bowl by (a) holding the bowl under the water jet or (b) by putting it on the floor in the right place
Fill box	Actor puts sawdust including grain and/or little food pellets in a box or bowl
Fix paper	Fix paper (typically a paper bag) to the grid, to a branch, or to a rope by bending the paper over one of these objects, then twining the ends together
Flap lip	Flap upper lip up, so teeth and upper gum are visible
Flee	Actor moves as fast as possible, thereby seems to lose its normal caution
Follow	Animal coordinates his movements with his partner, often moving closely behind the partner in the same direction (or leaving, e.g., the same nest shortly (<5 s) after the partner did)
Gathering	Mother pulling infant towards her. "Hold out hand" is often followed by "Gathering"
Genital inspection	Actor brings his face close to the genital region of a partner or touches it with a finger
Genital self-inspect	Touching vulva or penis with finger(s) or foot and then sniffing at it. Or rubbing genitals on an object and then sniffing the contact place
Gnaw wrestle	2 orangutans rolling over one another, pushing, hitting, tugging each other by the hairs of the neck (for example). Gnawing consists of pushing the bared teeth on to a hand or a foot (e.g., face, throat, and breast are seldom touched)
Grab	Grab objects (e.g. wood wool, paper bag, food, stick) with hand, foot, or mouth. In context of food "grab" is only stated, if animals doesn't immediately start feeding but is moving around with the grabbed food instead
Grasp	Grasp partner by the hair or limb and holding on
Gymnastics	Various activities (giving the impression of being non-functional) and locomotor patterns that are not oriented in a particular way with respect to a partner (could also be termed self-play)
Hand wrestle	Two individuals are lying next to each other, one extends a hand/foot to touch the other's hand/foot, the other grasps the partner's foot/hand and both try (without much force) to release the other's grip
Hang	Hanging without moving, on grid or rope, with 1–4 extremities grasping the grid or rope. If actor is hanging, supported by both arms with limbs fully extended, this is "posturing hanging". Special and distinct forms of hanging are also "hang exposed" and "dive"
Hang exposed	Actor is hanging with legs sideways up and both feet grasping the grid above, sometimes with one hand also grasping the grid above. The genital region is exposed
Head jerk	Fast jerky movement with the head towards a partner
Hit object	Strike fist quickly downwards from above on to an object
Hitting	A single stroke with the extended hand, brought downwards from above and landing on the head or on the shoulder of a partner

Table 4 continued

Behavior	Explanation of behavior
Hold out hand	Actor extends his arm in the direction of a partner and maintains that position for some time. When the juvenile screams, the mother holds out her hand preliminary to "gathering" it
Horizontal bared-teeth face	Strong retraction of the mouth corners and lips, thus exposing the teeth and gums, while the jaws remain closed
Join	Animal moving towards another one and stopping within an arm's reach distance; the other animal does not leave, they are staying together for some time. Joining a partner also means remaining (sitting or lying) next to it. If animals simply come close to another one, e.g. while they are feeding, grabbing food, this is not "join". "Join" ends if one of the animals moves away, or if both are involved in an active behavior
Knock	Knock on glass with a finger (typically with the pad of the forefinger) 2 or 3 times quickly in a row, usually when a visitor is there
Knock self	Knock with a finger several times in a row against own head/ear
Leaf gloves	Using leaves as gloves to handle nettles or other spiny food
Leave	Animal leaves the immediate surroundings of the partner at a normal, smooth pace
Lie	Lie on back or on belly, in nest or on ground. Animal may either watch the surroundings or sleep. Most of the animal's weight is supported by its torso, and the animal is in a horizontal position, its body reclining somewhere
Lift	Lift, e.g., wood wool, paper bag, and then drop it shortly afterwards, then usually looking (for food) at the place where the lifted object used to be, or looking at the object in some cases
Lift cover off someone	Lift cover (e.g. paper bag) off someone else to see who is beneath it
Load and fold paper	Put sawdust containing little food items (e.g. pellets or grains) on a piece of paper, and then fold paper so it can be carried away like a bag
Look at mouth	While holding the face very close to that of the partner, the actor looks intently at the other's chewing mouth. The actor's under lip is often slightly protruding and he may hold an open hand under the partner's chin, without touching it
Look at partner	While holding the face very close to that of the partner, the actor looks intently at the partner: in contrast with "Look at mouth" the partner's mouth is not chewing, and the actor does not look at the partner's mouth only
Look at tool-user	While holding the face very close to the partner that is manipulating an apparatus with a tool, the actor looks intently at the partner or the tool or the apparatus
Look up-around	Animal looks up from what it is doing (e.g. feed) and is looking around
Manipulate apparatus	Manipulate an apparatus (enrichment task). Note type of apparatus and tool (typically a stick) used, and whether actor is successful (s) and provides himself with the bait (s+), another animal takes it (s−), or actor is not successful (ns)
Mold	Molding paper or cardboard in bowl that has been filled with water before, then bring the molding mass to the mouth from time to time, chew it
Mouth–mouth	Mouth-to-mouth contact: Press the (slightly opened) mouth on that of the partner
Nest-building with paper and wood wool	Actor is building a nest without branches, usually on the ground or a platform. Actor uses wood wool and uses pieces of paper (which it typically produces before: "Rip paper"). On tree/rope no nest building is possible (only cushioning), whereas on ground/platform nest building and cushioning is possible
Nest-building with twigs	Consists of breaking and bending twigs and roughly interlacing these to form a platform
Nest-building with wood wool only	Actor is building a nest with wood wool only (without branches or paper), usually on the ground or on a platform. If animal only quickly uses wood wool, then the behavior is called "Nest cushion", nest building must last at least 10 s to be defined as such
Nod	Nod with head up and down with a regular rhythm and quite fast
Open paper bag	Actor opens a paper bag and holds its head inside
Open-mouth bared-teeth face	Lips and mouth corners are drawn back, exposing the teeth, but in this element the mouth is widely opened
Paper forehead	Push paper on forehead, followed by taking paper in mouth
Urinate on someone	While urinating another animal is hit
Pick nose	Elaborately picking own nose
Pick teeth	Elaborately picking own teeth
Pick with mouth	Actor is gently picking with its mouth the fur of another animal

Table 4 continued

Behavior	Explanation of behavior
Pirouette	While standing, actor is turning around its own axis (like a pirouette of a figure skater)
Play with object	Animal is handling an object (e.g. paper), doing various activities with that object that are giving the impression of being non-functional
Play with someone	Various activities, giving the impression of being non-functional, (as for "Gymnastics"), but another individual is involved and follows
Play with water	Actor is splashing or otherwise playing with water
Pluck lip	Actor is plucking at its lip with a finger
Poke hole	Actor pokes in small hole with finger, and then licks the finger
Posturing standing	Body is exhibited at maximal size: Actor stands erect, bipedally with extended arms and legs. Actor typically stands on a rope with both legs while his arms are hanging from another rope or the grid above
Press to self	Actor presses the child to her body. May follow after "Gathering"
Prolonged Pulling	Two animals are pulling on the same object against each other, e.g. pulling a twined paper bag, for a prolonged time (more than 5 s)
Push away	Push a partner away with hand or foot
Reel lips in	Actor reels lips in with closed mouth
Rip paper	Animal rips paper: Actor holds paper to the mouth and makes a small crack with the mouth, and then the paper is ripped in two pieces with the hands afterwards. Occurs in context with nest building
Rolling object	Actor is rolling/pushing an object/heap (e.g. wood wool) in front of him, or dragging it behind him (likely to be because it is too much to carry), object is in contact with the ground
Rolling sideways	Rolling sideways (not over head as in "Somersault")
Roundabout	Riding "roundabout" on a big bowl or around a post
Rub own genitals on other's	Actor is rubbing its genitals against the genitals of another animal
Rush after someone	Actor is rushing after a partner who is fleeing. This behavior is performed at very fast speed, in contrast with "Follow"
Scratch	Fast movement of fingertips over some part of the body. Actor doesn't look at body part where it is scratching, unlike in "Grooming"
Self-covering	Actor covers itself, typically with a paper bag, using it like a blanket. Animal is sitting or mostly lying under it
Self-decorating	Pieces of vegetation or objects like paper or wood wool are draped around the neck or put on the head, or held in an extended arm above the head
Self-grooming	Animal runs his fingers or the back of his hand through his hair against the direction of growth; also picks things with his fingers or mouth, looks in direction of the treated region
Shake	Shake an object (e.g. rope)
Shake hand	While letting the arm hang, animal shakes hand and wrist (seems to occur when animal is impatient, e.g. during or before manipulation of an apparatus, or when awaiting feeding
Share food	Actor is apparently offering the food and willing to share it. This "food-offering" is indicated by the actor not making a movement away, but having the hand that is holding the food in a posture not hidden by the body, but instead making a movement with the hand towards the partner so it can easily bite or pull a piece of food off
Silent-pout face	The lips are pushed forwards while they are pressed together at the mouth corners, but slightly opened in the middle, to form a small round aperture
Sit	Sit on ground, rope, tree, or in nest. Animal may either watch the surroundings or sleep. Most of the animal's weight is supported by its rear end, and the upper body is in a quite upright (>45°) position
Sit big	Sit with 1 or 2 arms extended vertically above and hands grasp the grid above. Arm(s) are stretched, the underarm is extended in an angle of 90° or more from the body, the upper body is thus quite stretched also and the animal looks big
Sit folded arms	Animal is sitting with folded arms: hands clasp opposite arms above the elbow
Sit folded hands	Sit with folded hands: individual grasps with one palm of its hand the other palm of the other hand
Slide	Sliding down the rope by hands loosely clasping the rope
Social-grooming	Grooming a partner. (For further details on grooming see "Self-grooming")

Table 4 continued

Behavior	Explanation of behavior
Somersault	Turning somersaults forwards or backwards
Stand	Animal is standing still, not moving, either erect or quadrupedally:
	(a) Stand erect: Most of the animal's weight is on its legs, it may hold on to a tree/rope/grid with one or both of its hands
	(b) Stand quadrupedally: The animal is standing on all its extremities, the weight is distributed equally
Steal food	Opposed taking, owner tries to prevent the theft. But actor grabs food from another animal with his hand, or bites off a piece with the teeth, while the owner is turning away trying to protect the food and clearly not willing to give food away
Steal wood wool	Grab the majority of wood wool from a platform where another animal is sitting or lying
Strangulate	Twining paper around the neck, as if strangulating self
Struggle	Animal attempts to free himself from the grip or restraint exerted by a partner
Symmetric scratch	Exaggerated, long, slow, symmetric scratching movements with both arms at the same time
Take food	Grab food from another animal with hand or bite off a piece with the teeth, while the other animal does not do anything to prevent it and is apparently tolerating the theft
Take partner's limb in mouth	Actor takes an arm or foot of a partner in its mouth, very gently. It does not result in gnaw wrestling
Take object away from somebody	Actor takes the object (e.g. a stick, bowl) away from another animal
Throat pouch inflation	Orangutans (both m and f) may inflate the large cavernous pouch that lies anterior to their throat (it is suggested to represent a state of general arousal)
Throw object	Actor is throwing objects around, apparently not aiming for anyone or anything, but quite forceful
Tongue play	Consists of fast movements with the tongue backwards and forwards, the mouth is slightly opened. Usually performed in front of the glass pane or even in contact with it
Tool preparation	Prepare an object to use as a tool afterwards: making a tool
Touch	Touch another orangutan with hand, finger, or foot; or touch an object without grabbing the object
Tree-hole tool-use	Using tool to poke into small holes to extract honey
Lower lip forward	Actor is pushing lower lip and lower jaw forward
Vibrating lips	Animal's lips are vibrating
Walk bipedally	Walking erect on ground, with hands not holding on somewhere
Walk hand-in-hand	Walking with someone and holding on to the other one's hand
Walk on rope	Walking erect on rope, with the feet moving on the rope and the hands clasping another rope above
Walk quadrupedally	Walking on ground quadrupedally, thus all hands and feet contacting the ground, or only the feet contacting the ground but the hands holding on somewhere to balance or to swing the body forwards
Watch	Actor stops what he was doing, sits down and attentively watches another orangutan, or watches in a particular direction for some time
Wipe	Make wiping-movement with the forearm on the ground, wiping sawdust to a line and investigate it for food (usually kernels or grain)
Wrestling	Resembles "Gnaw wrestle", but it is distinguished on the basis of a passive or clearly uncooperative attitude by the recipient
Yawning	Usually starts with an extreme pouting of the lips, changing to an opening of the mouth, and ends with a widely opened mouth exposing the gums and teeth

Some of the definitions are from the ethogram of Rijksen (1978)

Appendix 2

See Table 5.

Table 5 First successful performance of a behavior for every subject: the latency (hh:mm:ss) from the beginning of an experiment till an individual's first successful performance of the potential innovations occurring in the experiments, with the innovator's latency in bold letters

Behavior	Ca	Dj	Lea	Oc	Sel	Ti	Tu	Xi
Dip stick	00:01:40	00:40:40		00:15:10	00:05:26		00:00:50	00:01:52
Branch scoop				02:42:00	**00:12:30**		00:32:25	00:20:15
Vegetable rod					**02:46:00**			
Twisted paper rod				10:13:00	**09:59:00**			
Paper squash	01:48:40			01:37:20	06:20:00	00:46:50	**00:39:15**	
Wood wool squash	03:46:00			00:43:40		**00:40:15**	00:42:50	01:10:30
Twig squash				08:10:00			**04:33:00**	
Fish				04:49:00		05:18:00	**00:11:17**	
Sponging	**01:44:00**			03:45:00		03:32:00	03:41:00	03:27:00
Clean with hand	00:06:02	00:00:05	00:10:05	00:04:10	01:46:15	00:08:00	01:00:20	00:42:05
Leaf napkin	01:16:00	01:15:12	01:40:00			01:27:39	**00:01:02**	01:51:10
Leaf body scrub	02:16:25	**00:14:30**		02:24:00	00:39:27	00:52:30		00:48:05
Rub off	00:46:15	**00:32:25**						
Clean sb with leaf	**02:14:00**							
Shield	01:24:40				01:19:15	01:34:35	**00:20:50**	

"Dip stick" and "Clean with hand" are not assessed as innovations

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