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## RESEARCH ARTICLE

## Contrasting Responses to Novelty by Wild and Captive Orangutans

SOFIA I. F. FORSS\*, CAROLINE SCHUPPLI, DOMINIQUE HAIDEN, NICOLE ZWEIFEL,  
AND CAREL P. VAN SCHAIK\*

*Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland*

Several studies have suggested that wild primates tend to behave with caution toward novelty, whereas captive primates are thought to be less neophobic, more exploratory, and more innovative. However, few studies have systematically compared captive and wild individuals of the same species to document this “captivity effect” in greater detail. Here we report the responses of both wild and captive orangutans to the same novel items. Novel objects were presented to wild orangutans on multiple platforms placed in the canopy and equipped with motion-triggered video cameras. The same and different novel objects were also presented to orangutans in two different zoos. The results demonstrate extreme conservatism in both Bornean and Sumatran wild orangutans, who gradually approached the novel objects more closely as they became familiar, but avoided contact with them over many encounters spanning several months. Their zoo-living conspecifics, in contrast, showed an immediate neophilic response. Our results thus confirm the “captivity effect.” To the various ecological explanations proposed before (reduced risk and increased time and energy balance for captive individuals relative to wild ones), we add the social information hypothesis, which claims that individuals confronted with novel items preferentially rely on social cues whenever possible. This caution toward novelty disappears when human caretakers become additional role models and can also be eroded when all experience with novelty is positive. *Am. J. Primatol.* © 2015 Wiley Periodicals, Inc.

**Key words:** novelty response; orangutans; wild; zoo; captivity effect

## INTRODUCTION

In recent years, interest in novelty response has soared because it is generally seen as a major source of behavioral innovations and creativity [Auersperg et al., 2011; Greenberg, 1990; Kaufman & Kaufman, 2004; Kaufman et al., 2011; Mettke-Hofmann et al., 2002; Reader, 2003], which in turn are regarded as a good measure of cognitive abilities [Reader & Laland, 2002; Reader et al., 2011]. Novelty response is usually described by two main outcomes, neophilia and neophobia, which are generally considered two independent mechanisms [Carter et al., 2012; Greenberg, 2003; Greenberg & Mettke-Hofmann, 2001; Hughes, 2007; Mettke-Hofmann, 2014; Mettke-Hofmann et al., 2002; Miranda et al., 2013; Pisula et al., 2012; Russell, 1973; Sabbatini et al., 2007]. While neophilia refers to the seeking, approaching, and exploration of novelty, neophobia refers to avoidance of, reluctance to approach, or even fear of, novelty [Greenberg, 1990; Mettke-Hofmann et al., 2006; Mettke-Hofmann, 2014].

The aim of this study was to examine how wild and captive orangutans respond to novel artifacts. As what is novel is highly context dependent, responses may differ both qualitatively and quantitatively [Heyser & Chemero, 2011; Mettke-Hofmann et al.,

2006]. Because we could not measure the subjects' internal state [Mettke-Hofmann et al., 2006], and thus could not estimate distress and fear, our focus here is on the observable behaviors. Various other studies have also estimated neophilia/neophobia as approach rates to novel artifacts and/or willingness to feed near them [Benson-Amram et al., 2013;

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\*Correspondence to: Sofia Ingrid Fredrika Forss, Anthropological Institute & Museum, University of Zürich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland. E-mail: sforss@yahoo.com

\*Correspondence to: Carel P. van Schaik, Anthropological Institute & Museum, University of Zürich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland. E-mail: vschaik@aim.uzh.ch

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Bergman & Kitchen, 2009; Mettke-Hofmann et al., 2002; Webster & Lefebvre, 2001).

In primates, most studies of novelty response conducted on captive groups describe neophilia [Addessi et al., 2007; Chamove, 1983; Ehrlich, 1970; Glickman & Sroges, 1966; Joubert & Vauclair, 1986; Visalberghi, 1988]. In contrast, the few available studies of wild primates report cautiousness toward novel artifacts [Menzel, 1966; Visalberghi et al., 2003]. To ensure that this difference reflects the contrast between wild and captive conditions, within-species comparisons are required. We know of only two such comparisons with primates. First, after a habituation phase of banana provisioning on platforms, Visalberghi et al. [2003] investigated reactions toward novel food and objects in a group of free-ranging capuchin monkeys, *Cebus apella*. In contrast to captive capuchins [Visalberghi, 1988; Visalberghi & Frigaszy, 1995], wild capuchins consumed very little of the novel food presented to them; furthermore, they delayed approaching both novel food and objects compared to familiar food. A second study, involving rhesus macaques, *Macaca mulatta*, compared captive with semi-free ranging individuals, with similar results [Johnson, 2000]. Thus, in contrast to the curiosity and neophilia reported from captivity, among wild primates novelty seems to elicit avoidance. Among non-primates, the only such comparison involves spotted hyenas, *Crocuta crocuta*, again with the same outcome [Benson-Amram et al., 2013]. Moreover, among primates, there is growing evidence for social influences on the integration of novel food items into feeding repertoires [Addessi et al., 2007; Leca et al., 2007; Schuppli et al., 2012; Ueno & Matsuzawa, 2005; Visalberghi & Addessi, 2000; Visalberghi & Frigaszy, 1995], suggesting that upon encounter with novelty, primates use social cues rather than risk-independent exploration.

Other differences between wild and captive primates in the cognitive domain are consistent with differential responses to novelty, although they may also have other causes. Some primate species are known to use tools only in captivity, and some species using tools in the wild only manufacture them in captivity [Haslam, 2013; van Schaik et al., 1999]. Wild orangutans (*Pongo* spp.), for instance, use a handful of simple tools, such as sticks and leaves, whereas their captive counterparts have a broader tool repertoire, perhaps because human-induced artifacts create a broader range of opportunities than possible with naturally occurring objects [Byrne & Russon, 1998; Russon & Galdikas, 1993; Shumaker et al., 2011]. Moreover, captive baboons, *Papio anubis*, performed better in problem-solving tasks than wild conspecifics [Laidre, 2007], a pattern also confirmed in spotted hyenas [Benson-Amram et al., 2013].

This captivity effect has mostly been explained with reference to environmental factors. Reduced

predation and foraging pressure provide captive individuals with a risk-free environment, abundant free time, and excess energy [Benson-Amram et al., 2013; Haslam, 2013; Kummer & Goodall, 1985; Laidre, 2007]. In addition, it has been suggested that the exposure to man-made objects reduces neophobia and enhances object handling [Benson-Amram et al., 2013; Laidre, 2007; van de Waal & Bshary, 2010]. Further, in some species the social environment also differ in captivity not only resulting in increased social contacts with conspecifics [Haslam, 2013], but also social influence on behavior caused by the ability to attend to humans [Fredman & Whiten, 2008; Hirata et al., 2009]. It is therefore worth exploring the role of novelty response in the overall cognitive differences between wild and captive conspecifics.

The purpose of this study was to compare the novelty response between wild and zoo-living orangutans in order to examine to what extent we could replicate the “captivity effect” in novelty reactions within this species. We tested novelty responses in two wild populations, one on Sumatra (*Pongo abelii*) and one on Borneo (*Pongo pygmaeus wurmbii*). We also did two different kinds of zoo controls, one in which the exact same items were used and one in which other novel items were used.

## METHODS

### The Wild Populations

The experiments on novelty response were conducted on wild orangutans in Indonesia at two study sites: Suaq Balimbing on Sumatra and Tuanan on Borneo. The study site of Suaq Balimbing is situated in the Kluet region of the Gunung Leuser National Park in the province of Nanggroe Aceh Darussalam (03°39'N, 97°25'E). The Tuanan research site is located in the Mawas Reserve in the Central Kalimantan province (2°09'S, 114°26'E). At Suaq, the experiment was conducted between November 2010 and April 2011, and at Tuanan between August 2010 and April 2011. During these periods, 28 orangutans were followed as focal subjects and regularly seen in the study area of Suaq Balimbing; eight adult females, two flanged males, four unflanged males, seven adolescents, and seven infants. At Tuanan, 28 individuals were regular subjects of focal follows; seven adult females, seven flanged males, two unflanged males, five adolescents, and seven infants. The procedures for these experiments were approved by the Department of Forestry and Nature Conservation (PHKA) of the Republic of Indonesia and complied with the American Society of Primatologists' (ASP) Principles for the Ethical Treatment of Primates.

During the time period of these experiments we exposed the orangutans in their natural habitat to



Fig. 1. Platforms and novel objects presented to the wild orangutans: A fresh made orangutan night nest (a); a platform nest made to present the novel objects in the forest (b); a quadratic red Swiss flag presented together with plastic fruits (c, d); plastic flowers (e), and an orangutan doll (f).

items they had never encountered before. The novel materials presented were placed upon natural-looking platforms high in the canopy at various sites in the center of the study area, where the home ranges of many known females overlap. Because wild orangutans are occasionally seen exploring old nests in search of insects or re-building them for their own resting purpose, the platforms were established on a rattan base covered with leaves and branches of familiar tree species woven together to resemble orangutan nests, so the subjects would react toward the novel items rather than the construction itself (Fig. 1a and b).

In Suaq, 15 such platforms were placed at the most common travel height of orangutans within this habitat, 15–30 m [Prasetyo et al., 2009], in four different tree species: *Tetramerista glabra*, *Horsfieldia polyspherula*, *Parastemon urophyllus*, and *Sandoricum beccarianum*. The tree species and exact location for the platforms were selected based on ranging patterns and most visited feeding trees, where the orangutans passed by on a regular basis (Fig. 2). In Tuanan, where the forest canopy is lower, ten platforms were put up on a height of 10–15 m in the following species in the center of the study area (Fig. 2): *Syzygium* sp., *Notophoebe umbeliflora*,

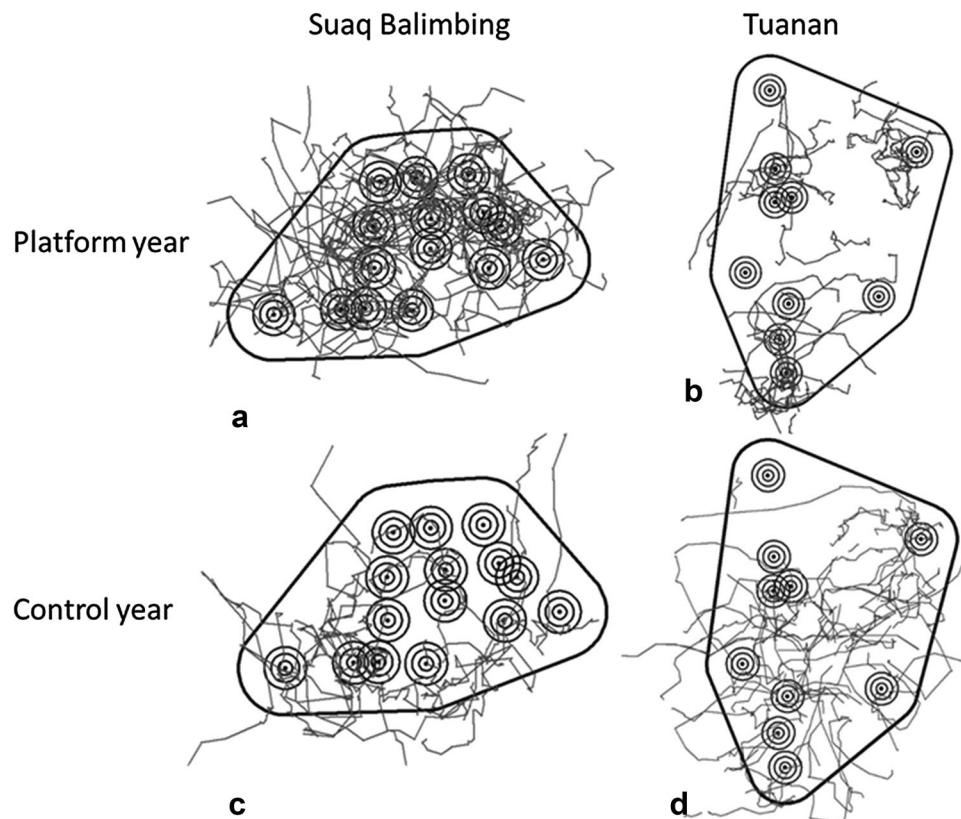


Fig. 2. a and b: Suaq Balimbing and Tuanan: orangutan travel routes and passes by the platform locations (30 m, 60 m and 90 m) during the experimental time period 2010–2011. c and d: Suaq Balimbing and Tuanan: travel routes and passes by the platform locations (no platform) during the control period (Suaq Balimbing: 2013–2014, Tuanan: 2012–2013).

*Shorea parvistipulata*, *Dyera lowii*, *Neoscortechinia kingii*, *Sandoricum borneense*, and *Payena leerii*.

The novel objects presented on the platforms were yellow, white, or pink plastic flowers, a small red quadratic flag (Swiss) in combination with plastic fruits and a small plush orangutan doll (40 cm) (Fig. 1c–f). Plastic flowers were chosen because their colors stood out against the otherwise green canopy but also might be visually recognized from a distance as a potential food item. Orangutans occasionally feed on flowers from multiple different species familiar to them. The red quadratic flag represented a shape–color combination not naturally occurring in orangutan habitats. It was placed above the platform in order to draw attention to the location and the explorable plastic fruits on the platform below it. The orangutan doll could potentially at a distance resemble an infant sitting on a nest, but at closer proximity perceived as a novel stimulus.

During focal follows at both Suaq Balimbing and Tuanan throughout the experimental period, we recorded all approaches toward a platform within 30 m (the approximate distance at which objects can be seen in the mid-canopy) using standardized focal protocols and ad libitum data [Martin & Bateson, 2007]. Focal methods basically followed van Schaik [1999]; a complete description can be found at: [www.aim.uzh.ch/Research/orangutanetwork.html](http://www.aim.uzh.ch/Research/orangutanetwork.html). At Suaq Balimbing, we additionally recorded all approaches to <10 m to a platform, gaze direction if at <10 m and any other responses (when present) of the orangutan. In order to maximize data collection but also to control for human influences on novelty response, five of the fifteen platforms at Suaq Balimbing and four out of ten at Tuanan (one camera less due to technical problems) were equipped with small and inconspicuously placed infra-red-motion-detection video cameras (DVREye Pixcontroller, PixController, Inc, Murry Corporate Park, Export, PA). The cameras were installed to record videos both day and night; batteries lasted up to 3 weeks, mainly depending on the number of motion-triggered events. The cameras were situated 2 m in front of the platform to ensure covering all possible physical interactions on or with the platform.

### The Captive Populations

It may be difficult to compare wild and captive conspecifics, because zoo-living subjects have been exposed to a wide variety of artifacts, making it harder to decide what is truly novel for them rather than merely similar and thus somewhat novel. We thus use the term “novel” for artifacts never seen before by our subjects and adopted a dual approach. In our first control experiment with a zoo group, we used the same objects that had previously been tested in the wild populations. For the objects used in the wild, we chose natural-looking artifacts in order

to reduce the degree of novelty, as captive subjects may have more experience with artifacts in general. In an additional experiment on another zoo group, we presented subjects with two novel items of different categories, albeit different from the ones used in the wild, presented in the open. The data collected with the captive populations complied with the Swiss animal protection law and consisted only of non-invasive experiments and behavioral observations in accordance with the principles of the American Society of Primatologists (ASP).

The first control experiment was conducted on seven Sumatran orangutans, *P. abelii*, housed in the Zurich zoo: one unflanged male, one male infant, and five adult females, one of whom experienced her first pregnancy. The captive subjects were housed in an indoor enclosure of 480 m<sup>3</sup> connected with an outdoor area of 188 m<sup>3</sup>. Every morning these orangutans are briefly sent into their sleeping quarters or a smaller room while their enclosure is being cleaned. As the orangutans are let back into their main enclosure, they can encounter enrichment objects such as old footballs, rubber pieces, cardboard boxes, and paper sacks, within which food is occasionally hidden. These are provided routinely and the orangutans are very familiar with the cleaning process and the objects normally lying around in their enclosure. In order to keep everything as normal as possible during the experimental observations, in the morning after enclosure cleaning, the zookeeper placed the novel objects on the floor in the middle of the enclosure. The orangutans would enter their enclosure from different sleeping quarters at slightly different angles to the object location, but the objects were detectable from all different perspectives. We performed the novelty experiments during three continuous days in December 2011, presenting one type of novel object each day.

Based upon information by the keepers, this group of subjects had never encountered any of these or similar artifacts before. However, the red quadratic flag was excluded from the captive part of this study, because these zoo orangutans are provided with red rectangular paper sacks on a regular basis, and a red flag would therefore not represent any particular novel shape or item to them, and also was not needed to draw attention in the open enclosure. The experimental time was set to 1 hr, although in all sessions the experiments were discontinued earlier because the objects had been torn into small pieces. The enclosure was video recorded from two different angles throughout the experimental sessions with two SONY HDV handy cameras (Sony Corporation, Switzerland). Time to first approach until contact with the objects, exploration spans, defined as durations of the manipulations of the objects, and distances to other group members were recorded directly at the test sessions as well as subsequently from the videos. As a control condition we used the video recordings of one morning without any novel objects; the same data were collected on

interactions with objects familiar to the orangutans in this zoo. On this randomly picked day the familiar enrichment items were red paper sacks and cardboard boxes.

The second control experiment involved slightly different novel artifacts. It was conducted in February 2009 on seven Sumatran orangutans, *P. abelii*, housed in Frankfurt zoo. This group of captive subjects was kept in a 253 m<sup>2</sup> enclosure and consisted of one flanged male, three adult females, two immature males, and one immature female. In this data set each subject was tested individually, except for mothers with dependent offspring (the latter would not participate in the test). On any given day, one individual was tested with one novel item in their main sleeping quarter. The following novel artifacts were presented on a small open platform: a soft blue rubber ball (diameter 13.5 cm) normally functioning as a dog toy and an Osram LED light, as a control condition approach latencies towards an empty platform were used. The degree of novelty inevitably differed somewhat between the used artifacts: due to the subjects' previous experience with old footballs, the blue rubber ball might be less novel to them than the flashlight. All experiments were video recorded and analyzed using Mangold INTERACT 8 (Mangold International GmbH, Arnstorf, Germany).

All statistical tests were run in SPSS 19. For the wild population of Suaq we had more detailed data on distances and gaze direction; here we used binary logistic regression to calculate the minimal distance at which gaze directed toward novelty occurred, and thus the platform was noticed by the orangutan. We used Spearman rank correlations to investigate the relationship between approaches to novelty and exposure time. For the zoo population, we used the non-parametric Friedman's test, with additional post

hoc analysis [Siegel & Castellan, 1988] in order to correct for multiple comparisons with the same subjects. All the data on the captive study at Zurich zoo was taken by SF and in Frankfurt zoo by DH. The data on the wild populations was taken by SF and NZ, accompanied by well-trained field assistants. All the data used in the analyses from the wild involve distances; these are frequently measured by all field staff in our study and trained with calibrated poles.

## RESULTS

### Response to Novelty in Wild Orangutans

At Suaq Balimbing, platforms were maintained for 145 days and at Tuanan for 251 days. We first needed to exclude the possibility that there was something about the platform locations, other than the novel objects per se, that kept the orangutans from approaching them. The tree species itself, in which the novel objects were placed, did not influence the likelihood of approaching a platform ( $\chi^2(1,6) = 8.316$ ,  $P = 0.216$ ,  $N = 71$ ). Furthermore, we used ArcGis and GPS data to compare the range use patterns of the focal orangutans in the area with the platforms during the experimental period to a control period (the following year: Suaq Balimbing 2013–2014, Tuanan 2012–2013), when orangutans were followed during the exact same time period (and fruiting season), but in the absence of any platforms or cameras. We calculated the rates at which the orangutans passed the platforms at a distance of <30 m, <60 m, and <90 m during the experimental period (Fig. 2a and b), and repeated exactly the same analysis during the subsequent period, examining the passing of the same locations as where the platforms had been situated (Fig. 2c and d).

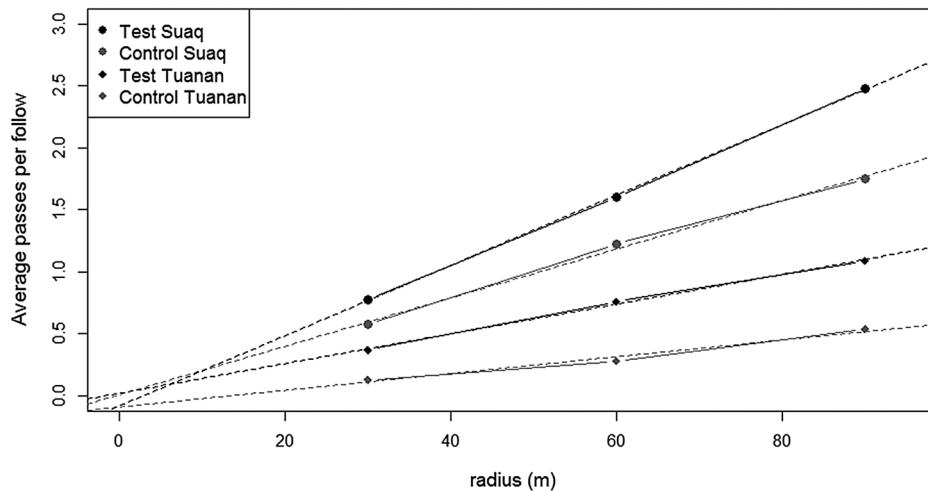


Fig. 3. Average passes per full-day follow by wild orangutans at 30 m, 60 m, and 90 m distance from the platform locations during the experimental year 2010–2011 (test) and during the control periods, when no platforms were present. The straight lines are fitted linear regressions. Note that they all approximately intersect the origin, suggesting no avoidance of the imaginary 30 m circle around the platform.

The average passes per focal follow for both study sites, Suaq Balimbing and Tuanan (test- and control period), are shown in Figure 3. The passing rates of the imaginary circles (30 m, 60 m, and 90 m) of the platforms during the control phase were slightly lower, because we had used the observed traffic patterns right before the experimental period to decide on the locations of the platforms in order to maximize the possible approach rate. However, there was no evidence that the imaginary 30 m circles around platforms were avoided (Fig. 3). We fitted regression lines to the average rate of passes per follow as a function of distance from the platform locations to assess whether movement was basically random. If there was avoidance of the closest circles to the platform, the fitted lines would intersect the abscissa at values well below zero. The regression lines approximately pass through the origin and their confidence limits all include zero, as expected when movement was random relative to platform location. Similarly, the observed 30 m points during the experimental period do not lie clearly below the line connecting the origin and the rates observed at 60 m and 90 m distance. Because the ranging patterns of the orangutans were random relative to the 30 m circle surrounding the platform, we conclude the orangutans showed neither active avoidance of, nor active attraction to the general area around the platforms during the experimental time period.

In the focal follows during the observation period, 59 cases were recorded at Suaq where an orangutan passed the platforms within possible viewing distance (30 m). The number of recorded approaches across the 28 focal followed individuals ranged from 0 to 10. In addition, the motion-triggered video camera traps captured 12 additional independent passes when no human was present (none of which involved physical contact). In total at Suaq 49 approaches to 10 m or closer were noted. At Tuanan, 20 approaches within 30 m were recorded during focal observations, plus none captured on camera (Table I). Because the focal data per individual were too sparse, we used the average pass rate (entering the imaginary 30 m circle) during all focal follows in the experimental period to characterize the average rate for the local population of coming close enough to the novel objects to view them. This rate, as extracted from GPS data in the platform area, was 0.78 per follow for Suaq and 0.37 for Tuanan (Table I). No individuals, apart from two adolescents Shera and Jerry (see below), were recorded to proceed until physical contact with the objects on the platforms during the experimental periods of 145 and 251 days for Suaq and Tuanan.

At Suaq, data was taken on close proximity and gaze direction toward the platforms. At this study site, from 59 recorded approaches to within at least 30 m, 49 were to within 10 m or less. Wild orangutans

**TABLE I. Approaches to the Platform by Wild Orangutans at Suaq Balimbing (Sumatra) and Tuanan (Borneo)**

Data recorded in the wild populations	Suaq balimbing	Tuanan
Number of approaches recorded during focal observations	59	20
Number of approaches recorded by video camera trap	12	0
Average passes (<30 m) per follow day	0.78	0.37
Average passes (<60 m) per follow day	1.60	0.76
Average passes (<90 m) per follow day	2.48	1.09
Number of experimental days	145	251
Number of days until first physical interaction with platform	110 (Shera)	74 (Jerry)
Number of focal follows (>6 hr) in the area during experimental time period	139	311

would direct gaze significantly more toward the platform while they had approached to within 10 m radius than when farther away (binary logistic regression:  $N = 59$ , Exp (B) = 0.861,  $P = 0.006$ , Fig. 4). This implies that at a 10 m distance, the orangutans had usually noted the platform. For all focal follows at Suaq Balimbing we calculated the approach rates (corrected for focal time of each individual) and found that as time went by and the novel objects thus became gradually more familiar, individuals were more likely to approach to within 30 m (Spearman's  $\rho$ :  $r = 0.260$ ,  $N = 48$ ,  $P = 0.081$ ,

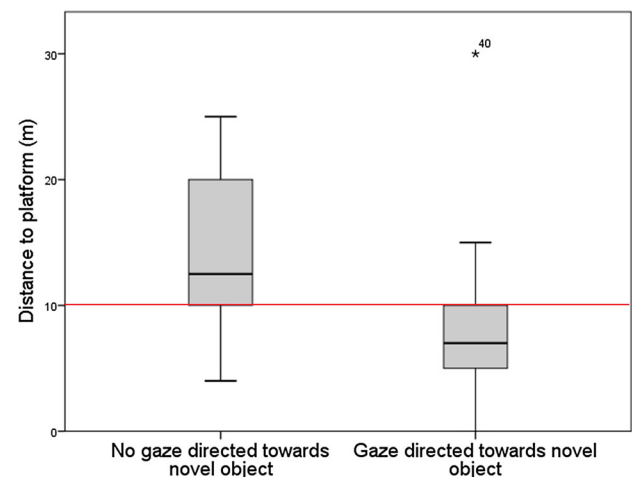


Fig. 4. Median distance to platform, provided the focal animal had approached to within 30 m to the platform, when it did not direct its gaze toward the platform with novel objects ( $n = 26$ ) versus when it clearly did ( $n = 33$ ).



Fig. 5a). Furthermore, we found that the minimum approach distances, provided there was a close approach to 10 m or less, decreased over time (Spearman's  $\rho$ :  $r = -0.439$ ,  $N = 49$ ,  $P = 0.002$ , Fig. 5b). Thus, as time of exposure increased the orangutans gradually approached the objects more closely.

The first and only time a wild orangutan at Suaq made contact with a platform and physically explored its contents was after 110 days. Similarly, at the study site of Tuanan the first and only physical approach was recorded after the novelty had been presented for 74 days (Table I). The adolescent female that explored the novel objects at Suaq Balimbing (Shera) only approached after her

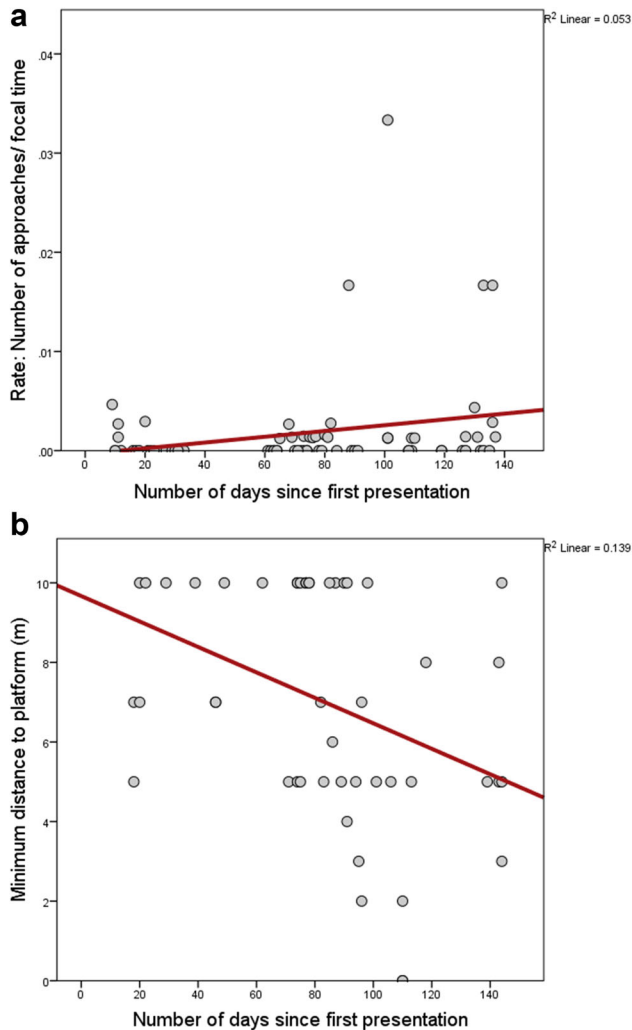


Fig. 5. **a**: Approach rates (number of approaches  $\leq 30$  m per hour focal time) for all individuals with at least five approaches recorded during focal follows as a function of the time elapsed since the novel objects were first presented (exposure time); **b**: relationship between all close approaches ( $\leq 10$  m) and exposure time. The data refer to the wild population of orangutans, *P. abelii* at Suaq Balimbing.

attention had inadvertently been drawn to the platform because she noted a human restoring the platform. After observing the person handling the objects on the platform from a distance, the female approached immediately after the human had climbed down. She moved onto the platform and picked up a plastic red apple and tried to bite in it. After several biting attempts she made a tool out of a small twig and poked at the plastic apple with her twig tool. After unsuccessful attempts with the twig tool she picked up a second red plastic apple and tried a third processing technique by striking it back and forth onto a branch. Shera's manipulation involved a feeding technique frequently used in her population, twig tool use [van Schaik et al., 1996]. Further, her exploration span resembles the one measured in captive orangutans handling the same objects for the first time (Fig. 6). Besides this one approach of physical exploration of the novelty, throughout the same time period at Suaq, 28 cases were recorded during focal follows, where an orangutan would explore a normal old nest, but no cases were seen where an orangutan handled the novel objects. The only individual in Tuanan who approached and physically explored the plastic flowers was a male adolescent (Jerry).

Both exploring individuals were adolescents. After their exploration of the novel objects no further physical investigation by the same individuals were recorded within the experimental time period. However, Shera passed a second platform with exactly the same objects on the same day only a few hours after she examined the plastic fruits for the first time. The second time around she approached to zero meters of the platform but only visually examined them and did not touch the plastic fruits presented there.

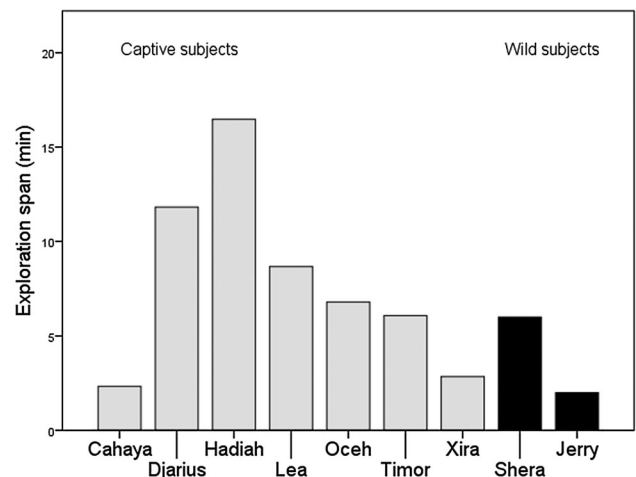


Fig. 6. Comparison of exploration spans (in min) between wild (black bars) and captive (gray bars) subjects handling a novel object: a plastic fruit.



Before these first contacts by the adolescents, it is highly unlikely that an orangutan at either site had approached to such close proximity that examination or manipulation of the novel objects would have taken place. First, in five of the 15 platforms at Suaq and four of 10 at Tuanan, such an event would have been recorded by the video camera, because the cameras did capture a diverse range of other animal species visiting the platforms. Second, not a single object was removed or dropped from the platforms, nor did the objects show any bite marks or other signs of physical exploration or disturbance. By using a crude estimate of approaches (mean number of 30 m passes per follow day times experimental days), by the end of the experiment the average orangutan at Suaq Balimbing had passed the platform location approximately 113 times, or 93 times at Tuanan, without ever handling the objects. However, it has to be noted that this estimate is based on the assumption of equal travel patterns for all individuals.

Neither Shera nor Jerry was unusually keen to approach the platforms: 0.44 per follow day ( $N=16$ ) and 0.25 per follow day ( $N=8$ ), respectively, close to the average values for their population. Shera's response was similar to that of the population in general, as she too approached the platform to within 30 m more as time went by (approach rate: Spearman's  $\rho$ :  $r=0.636$ ,  $N=13$ ,  $P=0.019$ ) and gradually decreased her approach distance when getting to at least 10 m (Spearman's  $\rho$ :  $r=-0.824$ ,  $N=6$ ,  $P=0.044$ ). By day 110, when Shera made contact with a platform, we estimate that she had passed by ( $<30$  m) roughly 48 times. The respective estimate for Jerry at day 74 at Tuanan would be 19 passes. Moreover, another adolescent at Suaq (Ellie) was observed within 10 m to a platform 10 times during the study period, but never physically explored the novel objects.

### Response to Novelty in Captive Orangutans

In Zurich zoo, the general approach latency towards novel objects was quite different: the Sumatran orangutans approached all novel objects tested within a few minutes (Fig. 7a). They had similar approach latencies for the novel objects as for the familiar objects in the control condition (Friedman's test:  $\chi^2(3)=5.229$ ,  $N=7$ ,  $P=0.156$ ). Similarly, the Sumatran orangutans housed in Frankfurt zoo approached the presented novel objects equally fast as the control condition when the platform was empty (Friedman's test:  $\chi^2(2)=0.519$ ,  $N=7$ ,  $P=0.772$ ) (Fig. 7a). In both zoo groups approach latencies varied individually, but were similar between the zoos despite the fact that experiments were performed in the group in Zurich and individually in Frankfurt. In the Zurich group, the wider distribution of approach latencies toward the novel objects versus the control condition, especially the orangutan doll, was probably caused by the fact that

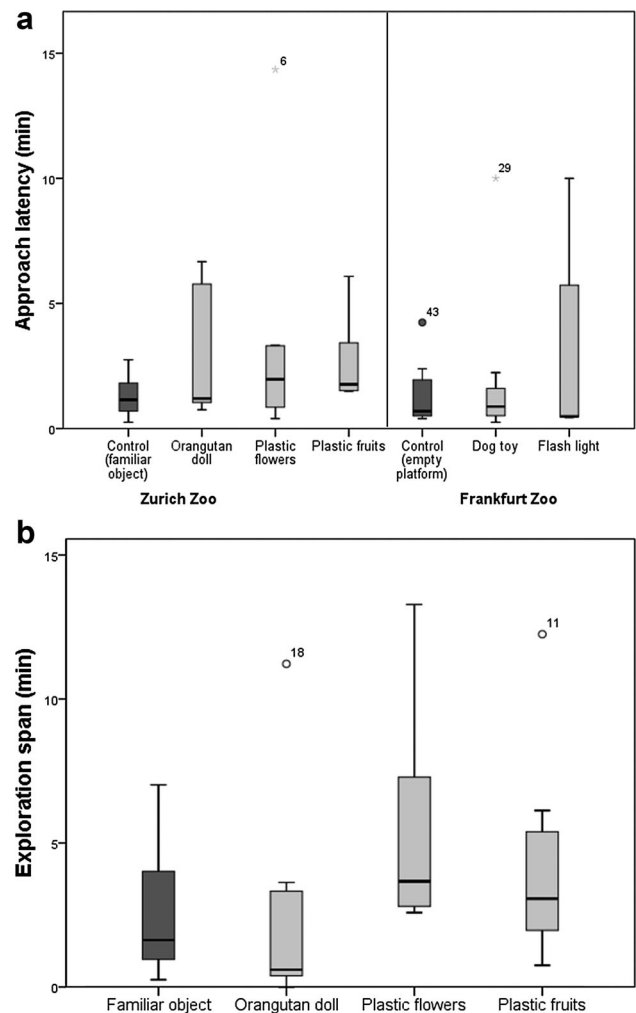


Fig. 7. **a:** Approach to contact latencies (in min) to novel objects by the orangutans in Zurich zoo (the same ones as used for wild orangutans) and in Frankfurt zoo (a blue rubber ball with holes, normally used as a dog toy, and a flashlight), compared with those to familiar objects or an empty platform, respectively, serving as a control condition; **b:** Total exploration time in minutes for the orangutans at Zurich zoo handling a familiar object and three novel objects.

only a single doll was presented in their enclosure. Therefore, not all individuals had access to it simultaneously, whereas the familiar objects and the bundles of flowers and fruits could be thorn apart for investigation by multiple individuals. In Zurich, because of the dominance hierarchy (S. Lehner, unpublished data), the two older females could not approach while the doll was being monopolized by the adult male.

In Zurich zoo, where familiar objects served as a control condition, exploration spans were significantly different between conditions (Friedman's test:  $\chi^2(3)=8.657$ ,  $N=7$ ,  $P=0.034$ ), but using post hoc analyses and applying a Bonferroni correction, pairwise comparisons revealed that none of the durations between the control condition

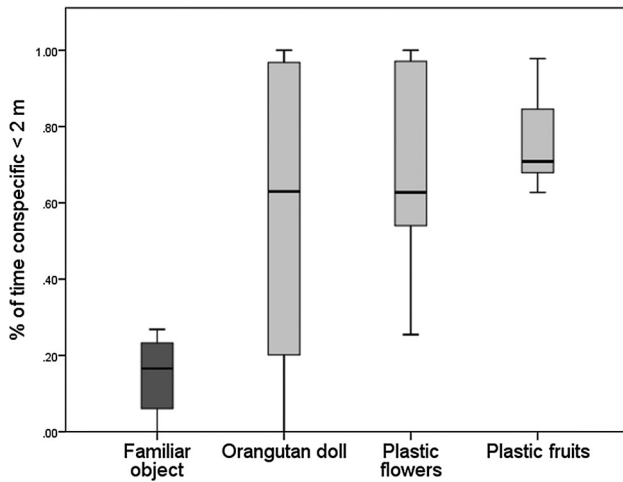


Fig. 8. Comparison of close social proximity (<2m) when handling a familiar object versus novel objects presented to the orangutans at Zurich zoo.

and the novel objects were significantly different (between all conditions the critical difference at  $P=0.05$ , corrected for multiple comparisons, was 12.74, Fig. 7b) [Siegel & Castellan, 1988].

Social proximity during novelty response in Zurich increased during the physical exploration of novel objects. A social partner was significantly more likely to be within two meters when it was engaged with the familiar paper bags or cardboard boxes (Friedman's test:  $\chi^2(3)=9.927$ ,  $N=7$ ,  $P=0.019$ , critical difference = 12.74, Fig. 8). During this closer proximity individuals often tried to grab the novel item from the individual handling it.

## DISCUSSION

### Wild Versus Zoo Orangutans

Wild orangutans were extremely unresponsive toward the novel artifacts. In fact, the novel objects did not elicit any particular reactions for several months, and therefore we could only report approach data, except for the two cases in which individuals actually handled the novel objects. Although not all platforms were supplemented with cameras, the absence of any physical contact by the orangutans is highly plausible. First, whenever we checked the platforms, the objects showed no signs of having been handled or bitten, and were never found to have been removed. Second, we recorded no contacts during focal follows, except for the two cases of physical interaction (which also left obvious signs of handling on the platforms). Closer approaches were more frequent as time went by (Fig. 5a and b), and these closer passes were accompanied by visual inspection at a distance, suggesting gradual habituation to the novelty but no approach proceeding to physical exploration of the

artificial objects. The two adolescents who eventually responded (one in each population) did so after several months of potential exposure. Indeed, contact latencies amounted to dozens of passes in the wild, even for the two adolescents who made contact after an estimated 48 and 19 passes (the latter necessarily are estimates, extrapolated from their mean number of passes per follow day). Although the others orangutans had passed the platforms with novel objects at <30 m about 100 times, they did not make contact with them.

In contrast to their wild counterparts, zoo orangutans approached almost immediately after noticing the novel objects for the first time, regardless of whether they were the same items as used in the wild (Zurich zoo) or other perhaps somewhat more novel objects (Frankfurt zoo), and irrespective of whether they were tested as a group (Zurich) or alone (Frankfurt). Thus, their contact latencies correspond to a single pass in the wild, and contact ensued within a few minutes at most. Zoo orangutans approached all the novel objects as fast as the control conditions of familiar paper sacks and cardboard boxes or an empty platform (Fig. 7a and b).

In the zoo setting the subjects also spent equal time exploring the novel objects as they did the familiar ones (Fig. 7b), suggesting interest in the unfamiliar even though no success in food search followed. Even if the zoo subjects regarded the novel objects as less novel than their wild counterparts, given their previous enrichment experience, they were clearly equally willing to approach and explore the novel objects as the familiar ones. This indicates that these groups of zoo-housed orangutans do not distinguish novel items as irrelevant nor potentially harmful compared to familiar ones.

The comparison, though producing a striking contrast, was not entirely unbiased. First, the animals tested in Zurich zoo were always in association, and it has been shown that association reduces neophobia so that novelty is approached faster in a group context than alone [Marzluf & Heinrich, 1991; Stöwe et al., 2006]. However, in the study performed at Frankfurt zoo each subject was tested individually and showed similar short approach latencies. Moreover, the orangutans at Suaq are also frequently in association [van Schaik et al., 1999], so differential sociality can only explain a small part of the difference. Second, novelty may cause stronger reactions in a familiar environment [Harris & Knowlton, 2001], and the zoo animals live in far smaller enclosures than their wild counterparts. However, the latter are obviously also very familiar with their habitat, [e.g., Janmaat et al., 2012], and continued to show no response toward the novel objects after dozens of passes. Thus, while the comparison cannot be made totally unbiased, the dramatic difference we observed is real and requires explanation.

### Explaining the Captivity Effect

This documented marked difference between wild and zoo orangutans in their response to artificial novel objects suggests that something about these two conditions fundamentally changes the response to novelty. So far, the main explanation has referred to time constraints. Due to the lack of predation pressure and foraging challenges, captivity has been argued to provide animals with a more relaxed time budget [Kummer & Goodall, 1985] or an excess of energy [Benson-Amram et al., 2013], allowing for more exploration. However, Benson-Amram et al. [2013] demonstrated that the higher problem-solving ability in captive versus wild spotted hyenas could be attributed to reduced neophobia rather than differences in time and energy. Thus, while the reduced attentional and perceptual load in captivity (due to lack of predation or the need to search for food and plan the daily routes) may free up animals to become more exploratory, having more free time per se does not explain reduced neophobia.

One key factor may well be risk [Haslam, 2013; Kummer & Goodall, 1985]. Wild orangutans cannot know whether novel objects are dangerous, and given their long life expectancy [Wich et al., 2004] may benefit from being conservative. Because exploration times themselves were similar for zoo and wild orangutans, once the latter approached the items (Fig. 7a and b), the difference between the wild and captivity is truly in the lack of avoidance of novelty. Risk assessment surely differed between the two conditions. Zoo-living animals only have positive experiences with novel items, which are usually food or playthings, and thus may have overcome any initial neophobia as a consequence of positive reinforcement with man-made objects. In fact given the less diverse environment of a zoo, the zoo subjects may have seen the artifacts as worth approaching and exploring. Their wild counterparts clearly did not. This may appear surprising, given that in the wild especially immature orangutans can spend up to 45% of their daily activity budget engaged in play, including play with familiar objects in their habitat [van Noordwijk et al., 2009]. On the other hand, exploration spans were similar between wild and captive subjects once an approach was made. If limited time and energy determined the response, this would not be expected.

While lack of risk and increased value of the objects may cause part of the documented difference between wild and captive orangutans in our study, we also propose social information as a complementary explanation. One obvious way to avoid risk when dealing with novelty is to use social information. Naive wild orangutans can attend to role models and heavily rely on social learning in the acquisition of their diet. Maturing individuals with abundant opportunities for social learning have come to rely

preferentially on socially learned skills to construct their cognitive abilities [the cultural intelligence hypothesis: van Schaik & Burkart, 2011; see also Herrmann et al., 2007; Whiten & van Schaik, 2007]. They thus follow experienced role models around and minimize independent exploration [e.g., orangutans: Jaeggi et al., 2008; Jaeggi et al., 2010; van Schaik et al., 2003]. As a result, naive orangutans tend not to interact with novel features in their environment until they have seen experienced role models interact with them. Rare food items are more likely to be unfamiliar to these naive immatures, and indeed in their natural environment, orangutan infants focus much more visual attention toward their mothers when the latter are feeding on food items that are very rare in the feeding repertoire [Jaeggi et al., 2010; C.S., unpublished]. Interestingly, unfamiliar objects in captivity also elicited social attention (Fig. 8). Thus, the availability of social information is consistent with the novelty avoidance in wild orangutans.

This account suggests that novelty avoidance is the natural response of wild orangutans. The availability of social information can help us understand the loss of novelty avoidance in captivity because in a zoo environment, human keepers serve as additional role models. Once these conditions are in place, the greater opportunity for social learning due to intense contact with conspecifics maintains and even boosts this captivity effect. Thus, we suggest that in species that have the ability to attend to humans as an additional source of information the neophilia seen in captivity arises in part because the novel items (objects, stimuli, and even spaces to some extent) are associated with humans and thus are implicitly approved for exploration. Indeed, semi-free ranging rhesus macaques have been reported to accept novel food faster when handed to them by humans than when they independently discovered it in their habitat [Johnson, 2000]. Likewise, orangutan orphans reared in rehabilitation centers and sanctuaries, experience human role models as replacement for their own mothers, and when in semi-natural conditions become very exploratory [Russon et al., 2009; Russon et al., 2010].

The two cases of contact in the wild are also consistent with a role for social information. When Shera, at Suaq Balimbing, approached and explored the novel objects, her attention had been drawn to them by a familiar human engaging with the objects (note that no physical approach was recorded in the absence of humans by the video camera traps). Furthermore, experiments have shown that infant orangutans refuse novel foods offered by unfamiliar humans unless they witness them being accepted by conspecific adults [Rijksen, 1978]. In general, the presence of conspecifics influence the acceptance of novel food in orangutans [Gustafsson et al., 2014; Hardus, 2012] a pattern also found in some other primate species, e.g.,

aye-ayes, *Daubentonia* [Krakauer, 2004] and capuchin monkeys, *C. apella* [Visalberghi & Addessi, 2000].

Future work should examine the range of species in which the captivity effect can be documented, and moreover what aspects of a captive environment causes novelty response and other behaviors to differ from that in natural habitats. The social information hypothesis predicts that in species with strong orientation toward tolerant role models in regular skill acquisition during development, but also gregarious, tolerant foraging per se, social attendance boosts interest in novelty. However, we stress that this idea is not meant as an alternative to the effects of ecological factors such as limited environmental stimulation, abundant free time and good physical condition. Regardless of the factors causing the captivity effect, an important unresolved question remains to what extent the documented cognitive differences between wild and captive populations [e.g., Laidre, 2007; Benson-Amram et al., 2013] can be attributed to different attitudes towards novelty.

### Neophilia and Cognition

Innovations have been shown to correlate with neophilia [Day et al., 2003; Webster & Lefebvre, 2001]. Wild orangutans avoid novelty. Yet, they have large innovation repertoires [van Schaik et al., 2006], and the Sumatran population at Suaq is the technologically most advanced orangutan population, showing a variety of tool uses, which are known to be based on innovations [van Schaik, 2004; van Schaik & Knott, 2001; van Schaik et al., 1996]. Admittedly, the one individual (Shera) at Suaq exploring a plastic apple used a stick tool to do so, but most others at Suaq ignored these novel objects, also after long exposure time. Moreover, we found no major differences between the Bornean and Sumatran sites with regard to reactions after passing within 30 m of a platform.

This comparison thus supports the idea that novelty response and high innovative ability do not necessarily go together [Brosnan & Hopper, 2014; Griffin & Guez, 2014]. First, as noted above, the attitude toward novelty and the tendency to explore are probably independently regulated at the proximate level. There were no differences between the wild and zoo individuals in exploration time, once the latter had proceeded to physical contact with the novel objects. Second, as suggested by the orangutan comparison, highly technologically innovative species, such as great apes, may well owe their large innovation repertoires to their efficient social learning, which strongly increases the chances of persistence of any innovations that happen to have been made [Koops et al., 2014; van Schaik et al., 2003].

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