

Research



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Feeding decisions under contamination risk in bonobos

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Threats from parasites and pathogens are ubiquitous, and many use pathways that exploit host trophic interactions for their transmission. As such, host organisms have evolved a behavioural immune system to facilitate contamination-risk assessment and avoidance of potential contaminants in various contexts, including feeding. Detecting pathogen threats can rely on different sensory modalities allowing animals to screen for a wide array of contaminants. Here, we present a series of experiments in which bonobos showed clear avoidance of contaminated food items, and were sensitive to risk along a contamination probability gradient. Across experiments, bonobos appeared to use multisensorial cues to inform their feeding decisions. In addition, bonobos showed reduced tactile, gustatory and tool use activities when in the presence of contaminant versus control odours in a challenging foraging context. Our experiments build on previous work conducted in Japanese macaques and chimpanzees aiming at a better understanding of the ways in which the behavioural immune system operates in primates.

This article is part of the Theo Murphy meeting issue ‘Evolution of pathogen and parasite avoidance behaviours’.

1. Introduction

All heterotrophic organisms must acquire the energy and nutrients necessary for survival and reproduction by feeding. This includes parasitic and pathogenic organisms such as helminths, protists, bacteria and viruses, which themselves often exploit the necessary trophic interactions of their hosts: common routes of transmission involve the faecal–oral, hand–oral, fomite–oral–lung and trophic (i.e. involving an intermediate host) pathways [1]. Therefore, foraging animals face a dilemma, because the same items that provide them with the nutrition and energy needed to survive and reproduce may also expose them to harmful agents that exploit such trophic interactions for their own survival and reproduction. How this trade-off between energy/nutrition acquisition and infection avoidance might influence foraging decisions has now been described in several species (e.g. oystercatchers [2]; cattle and sheep [3,4]; Japanese macaques [5]), though we are only beginning to scratch the surface in understanding the diversity and effectiveness of such strategies in nature, as well as the mechanisms by which they are generated.

Since threats from parasites and pathogens cannot exclude animals from feeding altogether, hosts (all animals are host to some parasite or another) are hypothesized to have evolved a behavioural immune system [6] to facilitate contamination-risk assessment and avoidance of potential contaminants. As such, animals must first detect and discriminate between the potential risks of pathogen acquisition associated with foraging. Detection can rely on different sensory modalities, allowing animals to screen for a wide array of potential contaminants (e.g. bodily fluids, soil). Numerous examples can be found in the literature describing such phenomena. For example, bacterivore nematodes (*Caenorhabditis elegans*) can differentiate edible bacterial lawns from pathogenic lawns via chemosensation and select the former as suitable forage [7]; reindeers (*Rangifer tarandus*) show

olfaction-based aversion towards food contaminated with conspecific or sheep urine [8]; and chimpanzees (*Pan troglodytes*) use tactile cues to avoid feeding on substrates that simulate the consistency of substances such as faeces [9]. Evidence is accruing to suggest that such avoidance responses are indeed common across the animal kingdom [10–12]. The Parasite Avoidance Theory of Disgust (PATD) was thus introduced to place the emotion of disgust into an evolutionary framework, suggesting that disgust evolved to help animals respond to and avoid matter that might harbour communicable pathogens and parasites [13], though whether other species experience similar emotions that drive such avoidance behaviour remains to be determined.

To specifically avoid the ingestion of potentially infectious agents, individuals must first detect (e.g. via visual and/or olfactory or other chemosensory cues) contaminated food sources and either refuse to feed on them [6] or process the contaminated items before ingestion [5]. Another strategy, widespread in humans, is to wash hands after contacting foods perceived as hazardous or eliciting disgust [14]. Furthermore, when external cues are not available, internal cues such as consistency and flavour can be assessed via other sensory modalities such as touch and taste, although these already entail a higher risk of exposure to hazardous agents. As such, other adaptive strategies exist to avoid the ingestion of potentially harmful food items. This includes food neophobia, the tendency to reject or exhibit increased caution around novel foods (e.g. [15,16]). Rats, for example, are known to be very cautious around novel food and ingest only small portions when encountering such items [15]. Falling ill after consumption initiates a potent conditioned (learned) taste-aversion response, making the rats likely to avoid such ingesta in the future. Such behaviour clearly illustrates the ‘omnivore’s dilemma’ [15]: the trade-off between nutrient/energy intake and exposure to parasites or intoxicants that mediates behaviour towards novel foods. Food neophobia in dietary generalists may, therefore, serve a complementary function to the behavioural immune system. The first direct evidence of a positive correlation between food neophobia and pathogen disgust was demonstrated in humans, with participants who rated themselves less likely to try novel and unfamiliar foods scoring higher on pathogen disgust [17] via the Three Domain Disgust Scale [18]. Further research is now needed to test whether these traits also correlate across individuals in other species.

Sex differences regarding infection and infection-risk aversion may also exist. Males of many species generally exhibit greater rates of infection and carry larger parasite or pathogen burdens than females, one reason being that androgens reduce immunocompetence but also affect disease resistance genes and behaviour [19]. Behaviours of concern for pathogen acquisition include inter-male aggression, dispersal and male reproductive strategies in general (e.g. the rut in male reindeers), many of which are testosterone-dependent. However, it has also been proposed that females simply invest more in health and longevity than do males [20]. Extending this idea to sex-biases in risk sensitivity during foraging, we might predict males to be less risk-averse than females, i.e. less sensitive to cues of potential food contamination. This prediction was supported by evidence from Japanese macaques [5], although another study found that female and male chimpanzees did not differ in their sensitivities to potential contaminants [9].

There are two primary mechanisms by which animals can avoid contracting parasites and pathogens: by avoiding

infected conspecifics and by avoiding contaminated foods. Pathogen and parasite avoidance behaviours have been described in a wide range of species in both social [10,21–27] and foraging [5,28–31] contexts. However, contamination-risk recognition and assessment in a feeding context remains largely unexplored in our closest phylogenetic relatives, despite the numerous infectious diseases we share with non-human primates (e.g. typhoid fever, gastroenteritis, giardiasis) and which are caused by the ingestion of infectious agents (e.g. *Salmonella typhi*, *Rotavirus*, *Giardia* spp.) found in contaminated water or food. Therefore, we expect to have evolved similar mechanisms of defence. To better characterize the cues that may be used by a non-human great ape species to indicate pathogen presence, we conducted five experiments investigating food neophobia and contamination-risk sensitivity based on visual and olfactory cues in bonobos (*Pan paniscus*). In addition to testing specific predictions for each experiment, as described below, we also investigated sex differences in response to contamination-risk, based on the considerations introduced earlier. Details are provided below in separate sections for each experiment, building on previous work conducted in Japanese macaques [5] and chimpanzees [9] hinting at the origins of human disgust and hygiene.

2. General methods

(a) Study site and participants

We tested semi-free-ranging bonobos at Lola ya Bonobo Sanctuary in Kinshasa, Democratic Republic of the Congo (see electronic supplementary material, tables S1 and S7, for details of each subject), from May to July 2016. Bonobos at Lola live in three separate rainforest enclosures (E1, E2, E3) and an outdoor forested playground (called ‘the nursery’) during the day, and are socially housed in dormitories at night. To facilitate maintenance, each outdoor enclosure has doors with a grid of metal bars through which bonobos can pass an arm and be examined by caretakers and veterinarians. In addition to fruits and leaves that are found naturally in their enclosures, bonobos are fed twice daily with 6.5 kg of seasonal fruits and vegetables, as well as sugarcane, soy milk, boiled eggs, yogurt and peanuts.

(b) General procedure and set-up

All experiments were voluntary, and were conducted in the morning or afternoon before feeding. Food items were placed on a table (80 × 40 × 50 cm) in front of the outer door of the enclosures. Bonobos could reach for the food by passing an arm through the square openings of the door or, alternatively, use tools to do so (figures 3–5). Individuals could not be completely isolated due to sanctuary policy. A trial or session would begin once a subject came to within 1 m of the experimental area and terminate after consumption of all food items, or alternatively if the subject moved further than 2 m away from the experimental area, or after 20 min had passed. All experiments were recorded with a Panasonic HC-W570M video camera mounted on a tripod, placed 2 m away from the experimental area, with the experimenter positioned behind. Across the different experiments, faeces, soil and rotten food (fruit, meat) were used as potential contaminants. While we could not exclude subjects from contacting them, they are regularly exposed to such contaminants in their

outdoor and indoor enclosures, except for rotten meat. Faeces came from conspecifics of a different enclosure than the one housing the target subject in any given trial. All subjects undergo regular health checks and anti-parasitic treatments, and were, therefore, monitored before, during and after experimentation, with no related ill effects being observed.

(c) Statistical analyses

The general statistical protocol involved generalized linear mixed-effects models (GLMMs) with binary and count response variables that varied with the type of experiment being conducted (see below for model details specific to each experiment). To test for an effect of age in our experiments, we classified the bonobos into 2 age groups: immature (infants and juveniles; 2–7 years, 24 individuals; $u \pm \text{s.d.} = 4.5 \pm 1.5$ years) and mature (adolescents and adults; 8–23 years, 40 individuals; 13.6 ± 3.7 years; electronic supplementary material, tables S1 and S7). For all experiments, we predicted that contamination-risk sensitivity would vary with age, with younger individuals being more exploratory and less sensitive to contaminant sensory cues than older individuals (e.g. [32]). All data were analysed in R v. 3.3.3 [33]. GLMMs with binary response variables were fitted using the package lme4 [34], and those with count responses were fitted using the package glmmADMB [35]. All GLMMs were fitted using maximum-likelihood estimation. We used the package lmerTest [36] to test the relative fits of models with and without the interaction terms using likelihood ratio tests (LRT); when interactions did not significantly improve model fit, they were dropped for parsimony and better interpretation of main effects. All raw data used in these analyses, videos of our experimental design, statistical tables and tables with details of participating subjects for each experiment appear in the electronic supplementary material.

3. Experiment 1: sensitivity to novel food

In a first experiment, we investigated whether bonobos may be food-neophobic—which to our knowledge has not yet been tested [37]—and if this could relate to food contamination sensitivity (experiment 2). We predicted that bonobos would either refuse to consume a novel food item, or at least avoid consuming the novel food item first among a choice of more common alternatives, as such behaviour may be risky. Indeed, food neophobia in humans and other omnivores is hypothesized to be adaptive, as it allows individuals to avoid ingesting potentially dangerous, i.e. pathogenic or toxic, food items. However, by doing so, omnivores may also miss the opportunity to ingest benign food items and thereby lose out on discovering novel sources of nutrition [15].

(a) Methods

Between 29 April and 6 May 2016, we presented 50 bonobos (24 females; electronic supplementary material, table S1) with three pieces of food simultaneously in each trial: plum (novel food item: S. Kwetuenda, personal communication), apple (rare and preferred when offered: [38,39]) and papaya (staple). Each food item had approximately the same size and weight (approx. 3 cm thick, 5 cm long, 25 g, with half-sizes being presented to infants), and similar compositions of calories and sugar (11.5, 13 and 11 cal/2.5, 2.5 and 2 g of sugar

in 25 g of plum, apple and papaya, respectively). The three food items were aligned on the experimental table 15 cm apart. The horizontal arrangement of items was alternated across trials to avoid issues arising from side biases. Subjects were tested only once and individually, either partly isolated with no other bonobos in sight, or with an audience of one or more others within 10 m of the experimental area. Three binary response variables were considered, indicating whether or not each food item was ingested, ingested first, and taken first by subjects in each trial. This last variable was created to distinguish interest in an item from motivation, to ingest the item, as this conveys different information about the intentions of our subjects and reactions towards novel or contaminated items. The fixed effects included food item, age category, sex, audience (presence/absence) and trial number (to account for previous exposure of subjects to the novel food item through the observation of others). Because we presented control and test items simultaneously, we tested for interactions between each of age and sex and the respective food items. This allowed us to determine whether differences existed in the sensitivities to these items across age and sex groups. We did not include an interaction between audience and food item as this variable was retained primarily as a control for variation in contexts across trials. Random effects included individual identity (because subjects could interact with several items in each trial and these interactions were recorded as separate but dependent events) nested within group origin (to account for potential group-level variation), and trial date (as the same experiment may have been conducted on different days). Models were specified with a binomial error structure and logit link function.

(b) Results and discussion

The statistical models including interactions did not outperform the models without them (LRT; ‘feed’: $\Delta\text{LogLik} = 2.65$, $\Delta\text{d.f.} = 4$, $p = 0.258$; ‘feed first’: $\Delta\text{LogLik} = 0.67$, $\Delta\text{d.f.} = 4$, $p = 0.856$; ‘take first’: $\Delta\text{LogLik} = 0.83$, $\Delta\text{d.f.} = 4$, $p = 0.799$; electronic supplementary material, table S2), so we retained the latter for parameter estimation. The proportions of feeding on apple, plum and papaya were 0.98, 0.94 and 0.76, respectively. The proportions of bonobos feeding on apple and plum did not differ significantly (GLMM; $z = -0.98$, $p = 0.325$; electronic supplementary material, table S3), although both were significantly more likely to be consumed than papaya (plum, $z = 2.56$, $p = 0.010$; apple, $z = 2.82$, $p = 0.005$). Bonobos ingested plum first significantly more often than both papaya ($z = 3.63$, $p = 2.8 \times 10^{-4}$) and apple ($z = 2.01$, $p = 0.045$), and picked up both plum and apple first significantly more often than papaya (plum, $z = 2.38$, $p = 0.018$; apple, $z = 2.56$, $p = 0.010$; electronic supplementary material, video S1).

Rather than being food-neophobic, then, our results suggest instead that these sanctuary-housed bonobos exhibit food neophilia, at least concerning novel fruits. Previous studies with other great apes have also shown low degrees of food neophobia in gorillas and orangutans [37]. In that study, the lack of food neophobia observed in gorillas was suggested to relate to digestive physiology: gorillas consume high amounts of plant secondary compounds and may, therefore, be less sensitive to the potential toxicity of novel plant items [37]. By contrast, lack of food neophobia in orangutans was explained by unpredictability in their nutritional

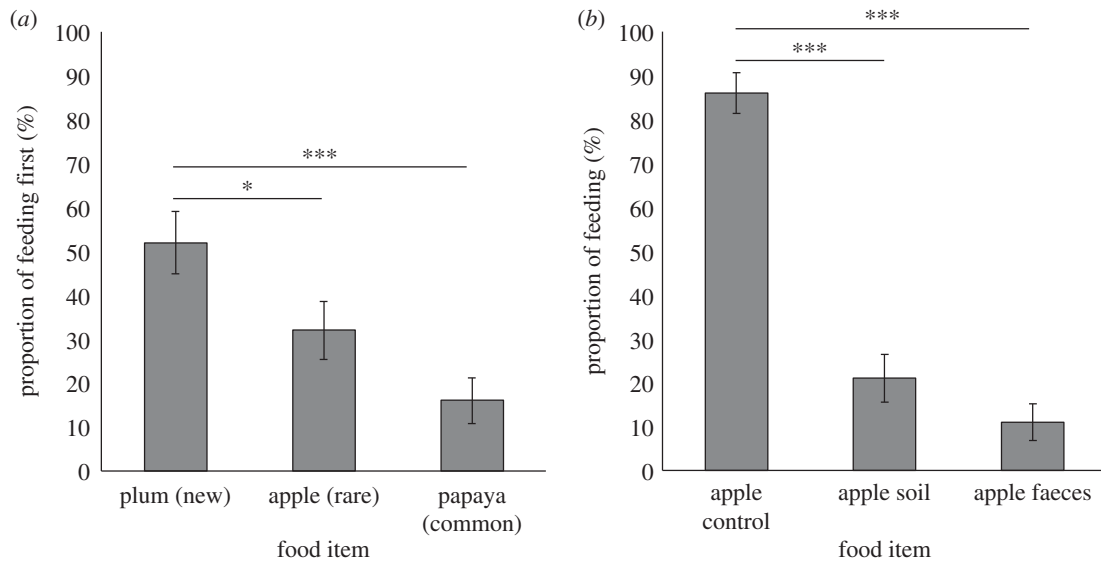


Figure 1. (a) Proportion of feeding first on the novel food item, plum ($p \pm \text{SEP} = 52 \pm 7.1$), on the rare food item, apple (32 ± 6.6), and on the common food item, papaya (16 ± 5.2) in experiment 1. (b) Proportion of feeding on the apple control (86 ± 4.6), the apple covered with soil (21 ± 5.4) and the apple covered with faeces (11 ± 4.2) in experiment 2. Column heights represent the proportion and error bars reflect the standard error of the proportion.

environment, i.e. strong intra- and inter-annual variation in fruit production, which may encourage orangutans to experiment with novel foods in times of food scarcity [37]. Neither explanation is likely to apply to bonobos, which lack such digestive specializations and inhabit a relatively unseasonal environment in nature (e.g. compared with chimpanzees [40]).

Because the novel food item was hand-placed on the experimental apparatus by the experimenter, rather than being discovered by the bonobos in their forested enclosure, it is unclear how generalizable these results might be, or how representative they are of animals living in natural conditions. Semi-free-ranging rhesus macaques, for example, are more likely to eat a novel food if it is provided to them directly by a human than if they were to discover the novel food in their environment [41]. While we are not aware of the initial reactions the bonobos had when green apples were introduced as a food reward by caretakers at Lola ya Bonobo Sanctuary, the fact that thereafter the item became one of their favourite treats [38,39] further suggests that they may not avoid novel fruits when provided by humans. Further experimentation would be required to test this possibility. Apart from these main results, we did not find any effects of age, sex, audience or previous exposure on feeding decisions, suggesting that fruit neophilia may be a common feature across individuals. However, the lack of diversity of novel food items presented limits our ability to make strong conclusions regarding the influence of such factors on predispositions towards novel foods more generally.

4. Experiment 2: sensitivity to contaminated food

In a second experiment, we tested whether bonobos are sensitive to contaminated food. For this, we presented three slices of apple simultaneously to each subject during each trial: one slice covered with soil, one slice covered with faeces and one slice clean (control). We predicted that bonobos would prioritize feeding on uncontaminated (control) over contaminated (faeces and soil) food sources. We also

predicted that more conservative subjects might refuse to consume the contaminated apple slices altogether, although the value of this preferred food item to the bonobos may override any potential risk aversion in these experiments [5].

(a) Methods

From 2 to 6 June 2016, we tested 56 bonobos (26 females; electronic supplementary material, table S1) in a three-choice task. The contaminant (soil or faeces; approx. 1 g) was spread with a spatula on the outside of the slice of apple (4 mm thick, 5 cm long, approx. 3 g). The three slices were aligned on the table and spaced 15 cm apart. The horizontal arrangement of items was again alternated across individuals. The experimental setup and the statistical analyses followed the same procedures as described in experiment 1, except that trial number was removed from the fixed effect structure as degree of novelty was no longer relevant.

(b) Results and discussion

The statistical models including interactions did not outperform the models without them (LRT; 'feed': $\Delta\text{LogLik} = 1.92$, $\Delta\text{d.f.} = 4$, $p = 0.429$; 'feed first': $\Delta\text{LogLik} = 1.39$, $\Delta\text{d.f.} = 4$, $p = 0.597$; 'take first': $\Delta\text{LogLik} = 3.00$, $\Delta\text{d.f.} = 4$, $p = 0.199$; electronic supplementary material, table S2), so we again retained the latter for parameter estimation. The proportions of feeding on the control, soil-contaminated and faeces-contaminated pieces of apple were 0.86, 0.21 and 0.11, respectively. Clean apples were thus consumed significantly more often than either soil-contaminated (GLMM; $z = -4.56$, $p = 5.2 \times 10^{-6}$) or faeces-contaminated ($z = -4.91$, $p = 8.9 \times 10^{-7}$) apples (electronic supplementary material, table S4). There were no significant differences in the likelihood with which the two contaminated pieces of apple were consumed ($z = -1.30$, $p = 0.194$). Bonobos fed on the control first significantly more often than on the piece of apple covered with faeces or soil (both $z = -6.07$, $p = 1.3 \times 10^{-9}$; figure 1; electronic supplementary material, video S2), while feeding on faecal-contaminated and soil-contaminated apples did not significantly differ ($z = -0.03$, $p = 0.978$). Subjects also picked up

the control piece of apple first significantly more often than the pieces of apple covered with faeces ($z = -6.13, p = 8.9 \times 10^{-10}$) or soil ($z = -5.82, p = 6.1 \times 10^{-9}$). The frequency with which either faecal-contaminated or soil-contaminated pieces were taken first was not significantly different ($z = 0.44, p = 0.659$), and there were no audience effects on foraging choices in any test (all $p > 0.200$; electronic supplementary material, table S4). However, age seemed to affect feeding decisions in this experiment, mature individuals tending to feed less on faecal- and soil-contaminated apples compared with the control apple ($z = -1.84$, both $p = 0.066$). Of the six subjects that fed on faeces-contaminated apple, four were infants, one was juvenile and one was adolescent. No adult fed on faecal-contaminated apples. Similarly, of the 12 individuals that fed on soil-contaminated apples, only two were adults. These results seem to indicate that age may play a role in contamination-risk sensitivity, with younger individuals being less cautious. There were probably too few occurrences of feeding on contaminated food to detect a stronger age effect in the models for this experiment.

Moreover, 14 subjects performed food processing behaviours (i.e. rubbing food on grass) after taking pieces of apple covered with soil or faeces and 15 subjects rejected (spat out) contaminated items after tasting them. None of these behaviours were observed after picking up or tasting the control apple. Together, these results provide evidence that bonobos are sensitive to food exhibiting visual, olfactory, tactile and gustatory cues of contamination. In contrast with previous tests on faeces-contaminated food avoidance in primates [5], the food item here was not merely placed atop the potential contaminant but instead coated with it, therefore amplifying the saliency of the contaminant as well as the risk associated with it, and probably lowering our subjects' attraction to it. The low proportion of feeding on contaminated food items here may also relate to anatomical specifications: great apes have long and thick fingers with proportionally short thumbs, which are well-adapted for suspensory locomotion but may limit refined manual food processing behaviours. In contrast, Japanese macaques rub, roll and wash food covered with sand, soil or faeces before ingestion [5], while tufted capuchins are known to rub unpalatable food within their hands on various substrates or rinse it (e.g. [42]). Food processing in great apes, on the other hand, mainly involves handling food with the mouth (e.g. [43]), which would automatically expose them to pathogens in the case of contaminated food.

(i) Food neophobia versus contamination sensitivity

We aimed to compare food neophobia with contamination sensitivity and determine whether subjects' responses to these experiments were similar across conditions. In experiment 1, subjects ingested the novel plum in 47 of 50 trials, prioritizing the ingestion of this novel food item over familiar ones in 26 of the 47 occurrences of feeding. However, in 30 of 50 trials, subjects initially picked preferred (apple) and staple (papaya) food items first over novel plum. In experiment 2, subjects avoided feeding on contaminated food in 37 of 56 trials, and even when they did, they prioritized feeding on the control items in 54 of 56 trials. In addition, subjects picked up the control items first in 51 of 56 trials. Ultimately, we could not include a statistical comparison of the responses in experiments 1 and 2, because there was little variance in subjects' decisions to feed on novel items, and little variance in subjects' prioritization to take or feed on contaminated items.

5. Experiment 3: degree of contamination sensitivity

In a third experiment, we examined whether bonobos could discriminate between different probabilities of contamination-risk. For this, we simulated a 'chain of contagion' experiment initially conceived to test human patients with obsessive compulsive disorder, who were asked to rate the contamination-risk of a pencil after it was placed in contact with an identified contaminated object, and then rate a chain of 11 successively placed pencils, with number 2 put in contact with the 'contaminated' pencil (#1), number 3 put in contact with 2, etc. [44]. Assuming that contamination-risk increases as the object (food here) nears the source of contamination in such a chain, we predicted that bonobos would show a gradient of avoidance in relation to contamination-risk.

(a) Methods

From 7 to 10 June 2016, we presented 52 bonobos (22 females; electronic supplementary material, table S1) with 6 slices of banana (7 mm thick, 3 cm diameter, approx. 5 g), the first one atop a fresh conspecific faeces (collected within 4 h prior to experimentation) and slices 2 to 6 were placed in succession from the position adjacent to the faeces until ca. 15 cm away, each in contact with the preceding slice (figure 2a). We alternated the arrangement of banana slices between the left and right side of the contaminant to account for potential side biases. All individuals from one enclosure were tested with the same faeces to avoid any confounds associated with varying source material. The statistical analyses followed the same procedures as for experiments 1 and 2.

(b) Results and discussion

The statistical models including interactions with 'feed' and 'take first' as response variables outperformed models without them (LRT; 'feed': $\Delta\text{LogLik} = 12.05, \Delta\text{d.f.} = 10, p = 0.008$; 'take first': $\Delta\text{LogLik} = 12.72, \Delta\text{d.f.} = 10, p = 0.005$; electronic supplementary material, table S2), so the former were retained for the analysis. In contrast, the model including interactions with 'feed first' as response variable did not ($\Delta\text{LogLik} = 5.36, \Delta\text{d.f.} = 10, p = 0.380$), so we retained the more parsimonious model without interactions. Although the models with interactions outperformed simpler models for feeding on banana slices and taking specific slices first more often than others, the details are somewhat difficult to interpret, perhaps because the number of banana slices being examined makes this a complex interaction. In fact, none of the interacting predictors explained significant portions of the variation in the response in either model (GLMM; all $p > 0.05$; electronic supplementary material, table S5). However, for the feeding model at least, the indication is that males may be more risk-averse than females regarding ingesting items in contact with faeces, but more likely to ingest slices further from it (slices 3 and 5 compared with slice 1, both $p < 0.100$; electronic supplementary material, table S5; figure 2b). In addition, immatures tended to be more risk-prone than mature individuals regarding consumption of slice 1, whereas there was little difference between age groups in consumption of slices 2–4 (all $p < 0.070$; electronic supplementary material, table S5; figure 2c). The results concerning interactions in the 'take first' model were even less convincing (electronic supplementary material, table S5).

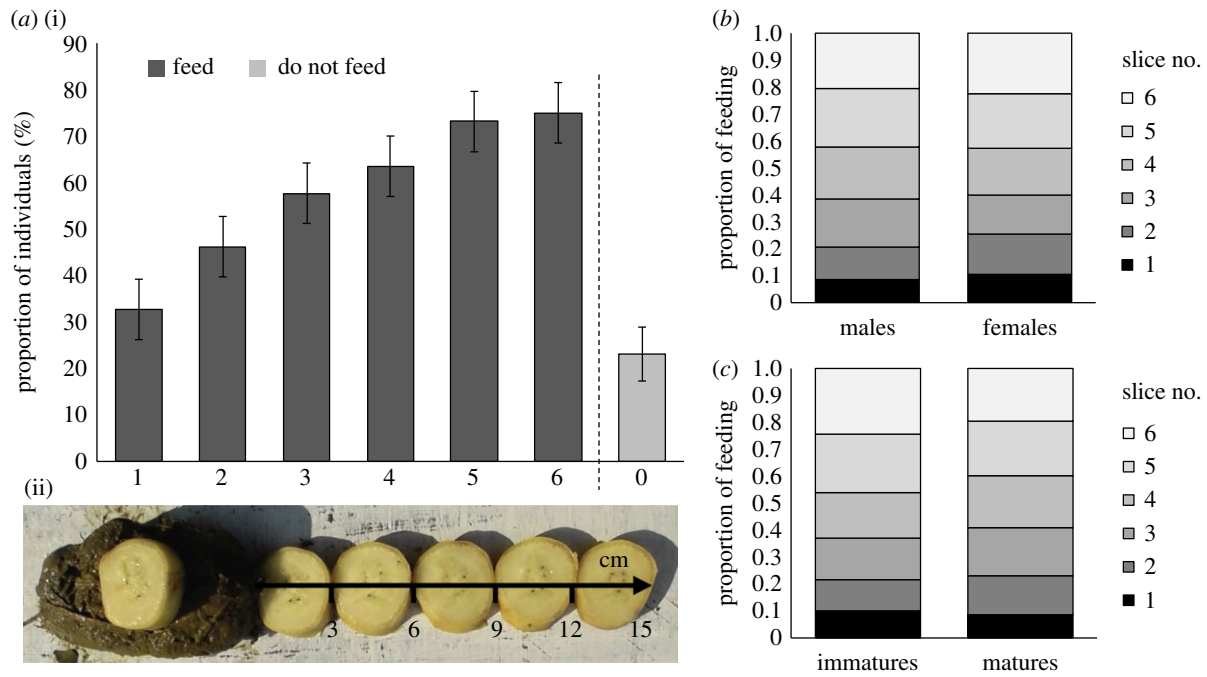


Figure 2. (a) Experimental set-up and proportion of individuals feeding on each slice of banana. (i) The proportion of individuals ($N = 52$) feeding on banana slices as a function of the distance to faeces. The column in light grey labelled '0' indicates the proportion of individuals that refused to feed on any of the slices of banana. (ii) The position of each food item, with banana slice 1 placed on top of the faeces and the distance of each slice from the faeces indicated along the arrow in centimetres. (b) Proportion of males ($N = 30$) and females ($N = 22$) feeding on banana slices at each position. (c) Proportion of immature ($N = 21$) and mature ($N = 31$) individuals feeding on banana slices at each position.



Figure 3. Sensitivity to previous contamination experimental set-up (experiment 4). (a) The experimenter put the 'contaminated' food in contact with a conspecific faeces (contaminant) for 5 s in front of the targeted subject while holding the control food in the other hand. (b) Both food items are placed on the table. (c) The contaminant is covered with a piece of cardboard. (d) The table is placed in front of the subject and the experimenter steps behind the camera.

Since our primary aim was to test for an effect of distance from the source of contamination on feeding decisions, and complex interactions with unclear outcomes such as those listed above complicate interpretation of main effects, we also report the parameter estimates for banana slice position from the models without the interaction terms. Subjects fed significantly less often on slice 1 compared with slices 2–6 (all $p < 0.020$; electronic supplementary material, table S5; figure 2a; electronic supplementary material, video S3). Similarly, they prioritized feeding on slice 6 first compared with slice 1 ($z = 3.07$, $p = 0.002$) and picked up slices 4–6 first significantly more often than slice 1 (all $p < 0.030$). Here again, we did not

observe any effect of other individuals' presence on foraging choices in the three models (all $p > 0.100$; electronic supplementary material, table S5).

These results indicate that bonobos can assess the probability of contamination across a set of items and use this information to inform their feeding decisions. Previous research has already demonstrated a relationship between feeding probabilities and distance to a source of contamination: wild mice treated with anthelmintics avoided food in contact with conspecific faeces [31], while another study found that wild mice (helminth infection status not considered) did not avoid food merely in proximity to faeces [45]. The gradient of

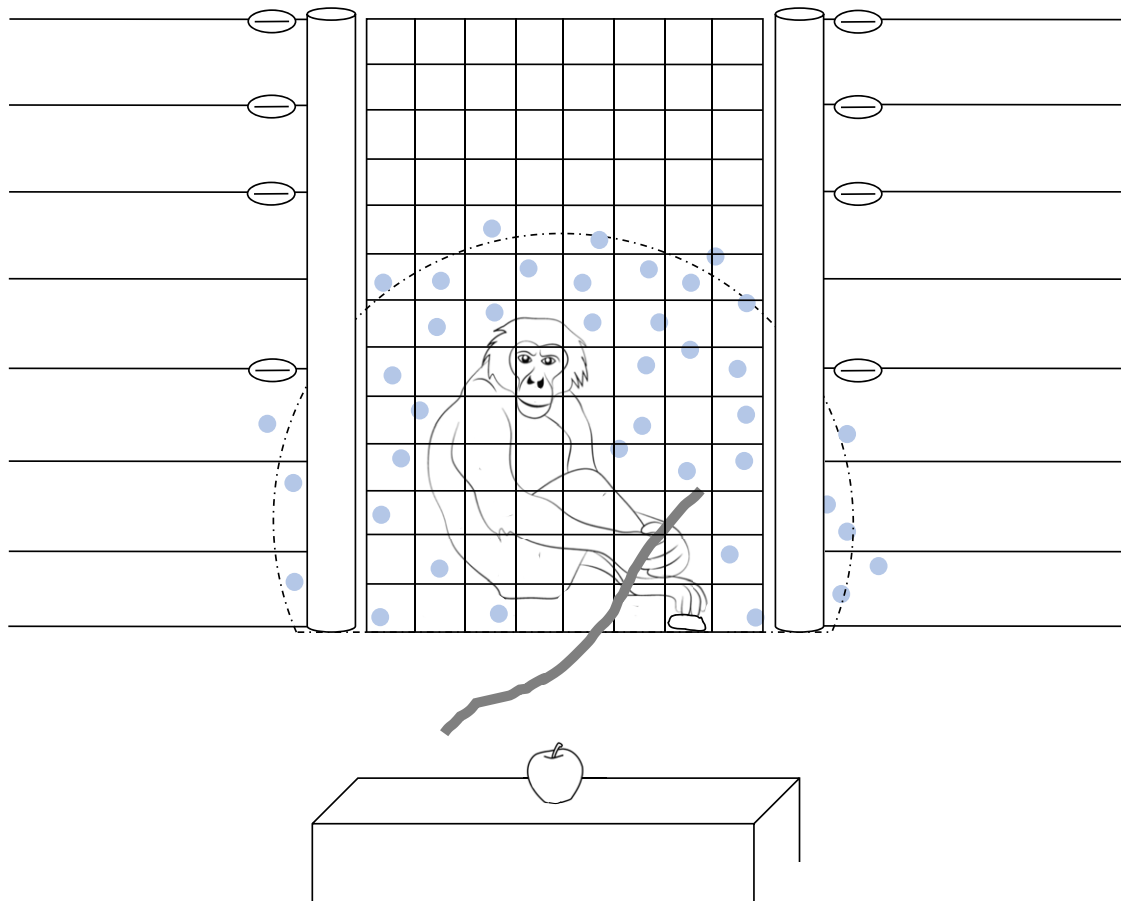


Figure 4. Experimental set-up for the olfactory tests (experiment 5). Conspecific faeces, detergent, spoiled banana, rotten meat or water odour was applied on the door. We recorded the number of contacts, gustatory investigations and instances of tool use in each session, with an apple placed just out of arm's reach at 1 m away, performed by any individual entering the 1 m experimental area around the door (dashed line). This was considered the distance within which subjects are likely to be exposed to the volatile compounds (blue spots) presented in each experiment. (Online version in colour.)

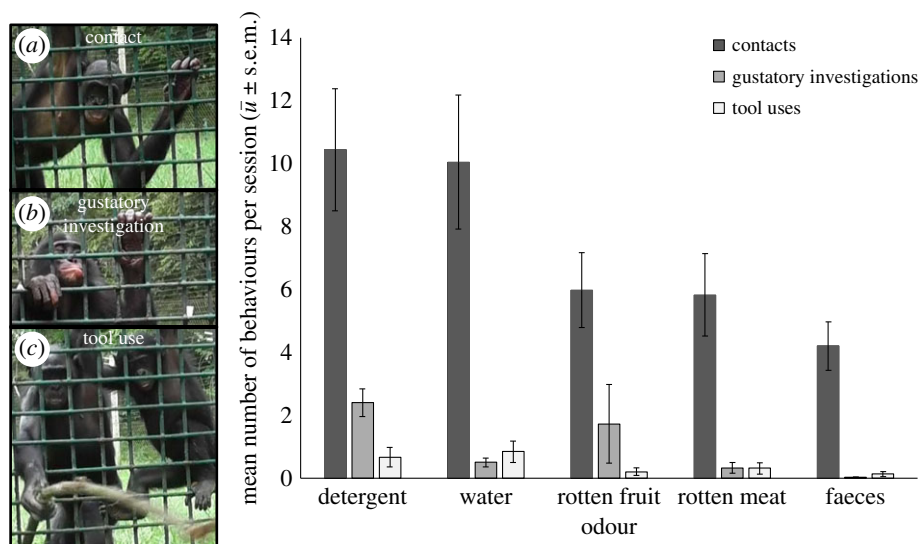


Figure 5. Mean number of contacts (*a*; dark grey bars), gustatory investigations (*b*; grey bars) and instances of tool use (*c*; light grey bars) per session during exposure to detergent, water, rotten fruit, rotten meat and faeces odours.

avoidance observed here in bonobos, which showed a higher aversion towards bananas closer to faeces, parallels results in a control group of humans, who rated the first pencils of a contagion chain as more contaminated than the following ones (see [44]). In our experiment, we also observed that 23% of the bonobos tested refused to take any of the banana slices

(figure 2*a*). As the risk of parasite contamination increases in the vicinity of faeces compared with control sites, the complete avoidance of feeding near faeces may be a conservative but effective strategy to reduce parasite acquisition [46], particularly because the immediate surroundings of faeces are expected to be contaminated by parasites [47].

6. Experiment 4: sensitivity to previous contamination

Experiments 2 and 3 demonstrate that bonobos generally avoid feeding on faecal- and soil-contaminated food, and can assess the probability of contamination along a spatial gradient near the source of contamination. However, both experiments provided visual, olfactory as well as potential tactile and gustatory cues of the contaminant. Here, we tested whether bonobos would store information about a previous contamination event and apply this information to their feeding decisions once visual cues of the contaminant had been removed, with other cues diminished. We predicted that, if bonobos can associate a contamination event with a food item and retain that information during testing, they should be able to discriminate between previously contaminated and control food items and avoid the former. By contrast, if certain cues, in this case predominantly visual, are necessary to elicit avoidance but are not maintained, bonobos would not be expected to show any preference between previously contaminated and uncontaminated food. The statistical analyses followed the same procedures as described above for previous experiments.

(a) Methods

From 11 to 15 June 2016, we presented 53 bonobos (23 females; electronic supplementary material, table S1) with two slices of banana on the table, spaced 30 cm apart. One slice was put in contact with some fresh conspecific faeces in full sight of the tested subject for a duration of 5 s. The faeces was then removed from the banana and covered with a piece of rectangular cardboard, and the table was placed in front of the enclosure door (figure 3). The position (left or right) of the contaminated slice of banana was alternated, and the experimenter alternated sides (and hands) relative to the contaminant between trials.

(b) Results and discussion

The statistical model including interactions with 'feed' as response variable came very near to statistically outperforming the model without them (LRT; $\Delta\text{LogLik} = 2.88$, $\Delta\text{d.f.} = 2$, $p = 0.056$; electronic supplementary material, table S2), while the model including interactions with 'feed first' as response variable significantly outperformed the model without them ($\Delta\text{LogLik} = 6.35$, $\Delta\text{d.f.} = 2$, $p = 0.002$). In contrast, the model including interactions with 'take first' as response variable did not outperform the one without them ($\Delta\text{LogLik} = 0.78$, $\Delta\text{d.f.} = 2$, $p = 0.458$). As such, we kept the models with interactions for 'feed' and 'feed first' as response variables, and the model without interactions for 'take first' as response variable. In the feeding model, despite that the interaction terms were retained, subjects of different ages (GLMM; $z = 1.50$, $p = 0.135$) or different sex ($z = -1.48$, $p = 0.139$) did not appear to differ in their feeding proportions with respect to previously contaminated and uncontaminated slices of banana (electronic supplementary material, table S6). However, immature and mature subjects differed in their tendencies to feed on contaminated versus control items first ($z = 3.36$, $p = 7.8 \times 10^{-4}$), with immature individuals being much more likely to feed on the contaminated slice first. Finally, subjects in general did not prioritize picking up the

control slice over the contaminated slice (GLMM; $z = -0.79$, $p = 0.431$).

To the experimenter, there were no remnant faecal particles visible on the surface of the contaminated slice of banana when presented to the subjects following the contamination event. Moreover, the previously contaminated side was facing the table, thus being initially out of sight to the subjects. Olfactory cues may have been present, and this may have contributed to the differences observed in the order in which the two items were consumed, as 71% of olfactory investigations of the contaminated food led to the observed preference for the uncontaminated control among adults. This suggests that when visual cues are not maintained and other cues are diminished, contamination avoidance is not or is at best only partly triggered.

Visual cues of faeces alone were demonstrated previously to induce significant food aversion in Japanese macaques [5] and humans [48,49]. We also recently tested the influence of olfactory cues of faeces, in the absence of visual cues, on foraging decisions in other primate species (chimpanzees: [9]; mandrills and long-tailed macaques: C. Sarabian *et al.*, unpublished data). Although tendencies to avoid food associated with faecal odour existed, they were considerably weaker and were not necessarily associated with food rejection as is seen with visual cues: while mandrills consumed food items associated with faecal odour significantly less often than in its absence, chimpanzees and long-tailed macaques did not. However, both species exhibited auxiliary behaviours that suggest additional caution was taken prior to consuming items associated with faecal odour: chimpanzees left the experimental area after being exposed to the odour but before being given access to the food (though they returned for the food later) [9], and long-tailed macaques processed the food before ingestion, which was not observed in the absence of this odorant. Further discussion of foraging behaviour in the presence of contaminant-derived odorants appears in the next section.

7. Experiment 5: sensitivity to odours of faeces and rotten foods

We aimed to further explore the influence of the olfactory environment on bonobo behaviour in this final series of tests. The strongest evidence to date for a contaminant-derived odour acting as a feeding deterrent comes from grazing ungulates. For example, cattle (*Bos taurus*) avoid eating artificial cereal pellets from a trough containing hidden conspecific faeces [50], and goats avoid hay treated with volatile compounds (pentane ether) extracted from cattle faeces [51]. Recent research has shown that primates use their olfactory system in more contexts than was previously thought, for example to detect olfactory cues of infection risk from bodily products and thereby avoid infected conspecifics [27,52,53], as is also seen in rodents [54,55]. Previous research on the impact of contaminant-derived odours on feeding behaviour has generally considered responses such as whether or not the food was eaten or the area vacated [50,51]. However, another line of reasoning that might reflect variation in risk assessment incorporates interactions between subjects and food items or the areas in which they are found. For example, individuals may engage in investigative behaviours targeting the item or even process the items in some way before ingestion (if consumed: [5]; and as seen above in experiment 4). Conversely, they might also be less inclined to

engage in more complex or challenging forms of food acquisition in the presence of contaminants.

In this experiment, we therefore presented bonobos with an apple just beyond arm's reach outside their enclosure to simulate a challenging foraging task, and simultaneously presented subjects with one of three assumed-to-be aversive odours (faeces, spoiled banana, rotten chicken), or alternatively with a neutral control odour (water) or a chemical control odour (detergent: Sumamousse[®], Marsavco S.A.R.L.). We predicted that bonobos would be motivated to attempt to reach the apple, as it is a highly preferred food, but also that they would be more cautious in the presence of contaminant-derived odours, for example exhibiting less contact with and fewer gustatory investigations of objects in the experimental area, and be less inclined to engage in complex problem-solving activities to acquire food. For example, bonobos are known to be proficient and motivated tool-users in captive settings, enabling them to solve challenging foraging tasks, though they rarely if ever use tools in the wild (see [56]). This design allowed us to test whether bonobos would be equally likely to gather and use tools in the presence and absence of contaminant-derived odorants.

(a) Methods

For each enclosure, we conducted three olfactory experiments (sessions with durations of 20 min each) for each of the five odours used. The first set of experiments were conducted from 9 May to 10 June 2016 (testing water, detergent and faeces; electronic supplementary material, table S7), and the second set on 15 and 16 June 2016 (testing water, rotten fruit and rotten chicken). On any given day, only one odour was presented to subjects of the same enclosure. These tests were conducted in a group setting, so multiple individuals could enter and interact with the experimental area simultaneously during a given session. Overall, 59 bonobos participated in our experiments, combining for a total of 325 individual trials ($\mu \pm \text{s.d.} = 4 \pm 1$ individual trials per enclosure per session and 34 ± 2 individual trials per odour with a mean number of 9 ± 1 engagements per individual per session; electronic supplementary material, table S7); one trial including all interactions performed by one individual in one session.

To produce the olfactory cues, we applied a specified contaminant using foam and/or a spatula to the enclosure door. We applied approximately 100 ml of either detergent, faeces or water, or 100 g of either spoiled banana or rotten chicken diluted in 10 ml of water in a plastic box or zip lock bag. In the case of enclosure 3, these amounts were halved as the door was half the size of the other enclosures. To attract subjects to the experimental area and subsequently test their motivations to acquire food, a table with an apple on top was placed 1 m away from the door. Subjects could interact freely with the experimental area, and use any means at their disposal to reach the apple, which as mentioned was just out of arm's reach without the use of tools. We did not provide tools in the experimental area, so subjects had to find and shape tools from somewhere in their environment. If an apple was dislodged from its position on the table (i.e. via tool use), the experimenter returned it to its original position. We withheld the apple for the duration of the session to maintain subjects' motivation, but provided the apple to a randomly chosen subject around the experimental area at the end of the session.

The first measure we considered was whether or not an individual entering the 1 m experimental zone would interact with the door in each of the conditions presented. In addition, for each 20-min session, all body contacts with the door, gustatory investigations (i.e. hand to mouth after contacting the door with the hand, or directly mouth to door) and instances of tool use (i.e. wood sticks) directed at or through the door by any individual entering the experimental area during this period were recorded (figure 4). If a subject contacted the door with its arm while using a stick, this was recorded as tool use rather than contact. Similarly, gustatory investigations were not simultaneously recorded as contacts. After each session and after the departure of all bonobo subjects, the enclosure door was disinfected with detergent and rinsed with water to remove the contaminant.

Models first included the probability of engaging with the experiment by contacting or tasting the door in the experimental area, or using tools to access the food reward through the door, as a single binary response variable. We then used the number of times each of these three behaviours was observed as a series of models with discrete count response variables. Observed counts of these behaviours across individual trials approximated the negative binomial distribution and were, therefore, modelled as such with a log link function. In these four models, we aimed to test for an effect of contaminant odours on the response variables, so we included odour condition (five levels), age category, sex and session number as fixed effects, and individual identity nested within group origin, as well as the date and session number (because there were three sessions per group per odour presented) as random effects to control for temporal variation and pseudo-replication within sessions, respectively. For this set of models as well, we tested for interactions between each of age and sex with odour condition.

(b) Results and discussion

(i) Overall interactions

The statistical model including interactions did not outperform the model without them, so we retained the latter for parameter estimation (LRT; $\Delta\text{LogLik} = 4.92$, $\Delta\text{d.f.} = 8$, $p = 0.277$; electronic supplementary material, table S2). Subjects that entered the experimental area showed a lower probability to interact with the door when the odour of a contaminant was applied than when either the water control was applied (GLMM; faeces: $z = -3.31$, $p = 9.3 \times 10^{-4}$; rotten chicken: $z = -2.42$, $p = 0.016$; spoiled banana: $z = -3.30$, $p = 9.7 \times 10^{-4}$; electronic supplementary material, table S8) or the detergent control was applied (faeces: $z = -3.25$, $p = 0.001$; rotten chicken: $z = -2.60$, $p = 0.009$; spoiled banana: $z = -3.21$, $p = 0.001$). In addition, the subjects' probability of interacting when detergent odour was applied was not significantly different from when the water control was applied ($z = -0.87$, $p = 0.386$).

(ii) Contacts

The model including interactions did not outperform the model without them, so we again retained the latter for parameter estimation (LRT; $\Delta\text{LogLik} = 6.58$, $\Delta\text{d.f.} = 8$, $p = 0.106$; electronic supplementary material, table S2). Test subjects had significantly fewer contacts with the door when in the presence of contaminant odours, compared with the water and detergent controls (GLMM; faeces: $z = -4.09$, $p = 4.3 \times 10^{-5}$; rotten chicken: $z = -2.71$, $p = 0.007$; spoiled banana:

$z = -2.24$, $p = 0.025$; figure 5; electronic supplementary material, table S8). Here as well, the number of contacts involving detergent odour was not significantly different from that involving the water control ($z = 0.77$, $p = 0.440$). However, irrespective of odour condition, males tended to show fewer contacts with the door than females ($z = -1.71$, $p = 0.087$) and immature individuals contacted the door significantly more often than mature individuals ($z = 3.15$, $p = 0.002$). Results also show that the number of contacts decreased with session number ($z = -3.03$, $p = 0.003$). This may reflect a sensitization (i.e. amplification of the avoidance response) effect if subjects became more averse to the odours presented over time, but a similar response may be predicted if subjects learn that they cannot access the food item and, therefore, become less likely to engage with the experiment over time (i.e. habituation).

(iii) Gustatory investigations

There were too few gustatory investigations to be able to retain interaction terms in the model; i.e. models failed to converge. As such, we ran the model without interactions. Bonobos showed fewer gustatory investigations when in the presence of faeces odour (GLMM; $z = -3.40$, $p = 6.7 \times 10^{-4}$; figure 5; electronic supplementary material, table S8) and to a lesser extent rotten chicken ($z = -1.65$, $p = 0.100$) compared with water control. However, they showed significantly more gustatory investigations in the presence of detergent odour compared with all other odours (all $p < 0.030$). Subject's sex and age did not significantly influence gustatory investigations in general (both $p > 0.200$). However, subjects tended to perform fewer gustatory investigations as we progressed with the sessions ($z = -1.82$, $p = 0.069$), suggesting a habituation or sensitization effect here as well.

(iv) Tool use

As was the case for gustatory investigations, there were too few occurrences of tool use across all sessions to be able to test interaction terms in the model. We thus ran the model without interactions. Bonobos showed significantly fewer instances of tool use in the presence of faeces odour (GLMM; $z = -2.82$, $p = 0.005$; electronic supplementary material, table S8), rotten chicken ($z = -2.12$, $p = 0.034$) and spoiled banana ($z = -2.34$, $p = 0.019$) compared with the water control. They also showed fewer instances of tool use in the presence of faeces odour compared with detergent odour ($z = -2.04$, $p = 0.042$). Otherwise, males used tools significantly less often than females ($z = -2.82$, $p = 0.005$) and immatures tended to use tools less often than mature individuals ($z = -1.87$, $p = 0.062$), as would be expected. We did not observe any habituation or sensitization effect in relation to tool use frequency across conditions ($z = -0.64$, $p = 0.520$). Note that some models failed to converge with session number and/or group origin included as random effects, in which case the offending variable was removed.

The olfactory cues that elicited the fewest interactions in our experiments were from biological contaminants that are known to be sources of infectious disease in humans and other animals [57]. However, bonobos did not avoid detergent odour, despite that the latter represents a condition involving a strong odour and that detergent can be toxic at high concentrations. This difference cannot be explained by degrees of novelty, as bonobos at Lola are exposed to faeces, rotten fruit and detergent

regularly, providing further evidence that it is the nature of the odour, not simply the presence of a strong odour itself, that impacted their behaviour.

Considering the age differences, immature individuals were more likely to contact contaminated objects than adolescents and adults, and this was irrespective of whether a contaminant or control odour was applied. Similarly, human children around 3–23 months are very curious and exploratory of their microenvironments, showing high rates of contact with the various surfaces and substrates around them [58]. Although we did not observe immature bonobos (infants and juveniles together) performing more gustatory investigations than mature individuals (adolescents and adults), when divided into four age categories, we observed that juvenile bonobos performed significantly more gustatory investigations than adults (data not shown), again matching the human literature in that behaviours such as hand-to-mouth, object-to-mouth or mouth-to-substrate are common among human infants who, by doing so, learn about their environments [58].

Previous research has shown that vertebrate, invertebrate and insect aversions to the odours of pathogen-containing food are often learned responses after experiencing post-consumption illness (see [32]). Such olfaction-triggered memory of illness-inducing substrates has been described as an example of imprinting (i.e. the rapid learning that occurs during a critical period early in life, and establishes a long-lasting behavioural response to a specific stimulus) in *C. elegans* [59], and may apply to other organisms as well. Thus, the lack of pathogen avoidance behaviours observed in immature bonobos could in fact be adaptive in the sense that it helps them develop the adaptive arm of their immune system. Yet, this kind of exploratory behaviour can also lead to intestinal diseases if soil-contaminated objects [60] or faecal particles [61] are put into the mouth, as well as intoxication if poisons are ingested. As such, one would expect that both innate and learned components of these aversions may have evolved to cope with exposure to materials exhibiting different degrees of risk; risk of fatality may elicit more programmed and/or less variable responses while less-threatening risks may elicit a more flexible set of responses. For example, most of our odour- and taste-based aversions are learned, which is hypothesized to give omnivores such as humans an advantage in adapting to novel environments [62]. However, the few known innate odour- and taste-based aversions concern decaying and dead bodies (e.g. putrescine and cadaverine in omnivorous zebrafish: [63]), the detection and avoidance of which would clearly be beneficial and adaptive [64].

While the presence of olfactory cues of contaminants allows animals to assess risks prior to contact with the source, tactile [9] and gustatory cues require that contact has been made, i.e. that contamination has occurred, and may, therefore, elicit stronger reactions to the stimulus, despite having less preventative value. This would explain why avoidance of most biological contaminant odours seems to be learned [32], while for some others, the aversive response appears to be present at birth—e.g. butyric acid (found in human vomit) elicits disgust-related facial expressions in newborn infants (e.g. [65]). Hence the distinction between taste avoidance and taste aversion—often used interchangeably in the literature, but which may require recognition of other cues (i.e. visual, olfactory) first, and be motivated by two different conditioned responses: fear and nausea, respectively, as found in rats [66]. Similarly, being exposed to contamination-risk cues may affect bonobo's

consummatory behaviour (i.e. eating a contaminated food item), but not necessarily their appetitive behaviour (i.e. processing a food item in order to make it edible).

Odours can mediate cognition and behaviour in different ways. For example, putrescine, a chemical compound produced by the breakdown of fatty acids in the decaying tissue of dead bodies, elicits innate necrophobic behaviours and primes animals for escape [67]. In a cognitive context, fear chemosignals (sweat) were shown to enhance performance in a word-association task in humans [68]. However, to our knowledge, no research has yet been conducted on how contaminant odours may affect cognitive performance. Our results suggest that odours from biological contaminants may alter the motivation of bonobos to use tools during a foraging task. It would, therefore, be appropriate to continue investigating this potential link between aversion and cognition in other settings.

8. Conclusion and perspectives

Across this series of experiments, bonobos showed avoidance of contaminated food items and sensitivity towards contamination-risk along a gradient of contamination probabilities. This sensitivity, however, seems to require the presence of multisensorial cues to enable them to associate a contamination event to a food item. In our last experiment, bonobos showed reduced tactile, gustatory and tool use activities when surrounded with contaminant olfactory cues in a food-motivated context. Altogether, these results are in line with the parasite avoidance theory of disgust, i.e. what we would expect if the bonobos had a system of disgust driving their behavioural decision-making. However, we do not test this hypothesis directly in our study, and therefore cannot conclude that bonobos were showing evidence of disgust in our experiments. Immature individuals (infants and juveniles) showed lower precautions in most of our contamination experiments, therefore matching human infant behaviour in similar contexts. Contrary to our predictions, however, we did not observe a female bias in contamination-risk aversion. Instead, males were even more risk-averse than females in one measure of contamination-risk sensitivity (experiment 3). Contrasting results have also been found in other studies, with no sex-biases in risk sensitivity observed in chimpanzees [9] but significant sex-biases observed in both humans (see e.g. [69]) and Japanese macaques [5]. In these studies, women showed higher disgust sensitivity [69] and female macaques exhibited higher rates of food processing behaviours and lower probabilities to feed when contamination-risk was present [5]. Future research investigating sex differences in other species of primates could shed light on the ecological or social contexts

responsible for these differences across species, and how they might relate to variation in health and fitness.

Finally, in addition to or perhaps even in concert with pathogen and parasite avoidance behaviours, other mechanisms may have evolved to reduce the probability of infection during contaminant encounters. Over evolutionary time, primates along with other animals have developed the ability to respond physiologically to exposure to contaminant-derived cues, especially when behavioural avoidance may be constrained by other factors such as parental care, reproduction or limited food resources. We know for example that humans physiologically react to disgusting stimuli via different sensory channels [70]. Exposure to odours of contaminants provokes heart rate reduction, indicating a vagal reaction and a decrease in blood pressure, both of which are hypothesized to prepare an individual for emesis, and therefore mimic the rejection of contaminants entering the body [70]. In addition, disease-avoidant ingestive behaviours may constitute one of several other physiological responses (e.g. thermoregulation, energy storage mobilization, immunity, sleep patterns) preparing the body to counteract pathogens by anticipatory immune responses (for example see [71]). Therefore, new avenues for research should focus on the physiological responses of non-human primates to contaminant-derived stimuli, at different contamination-risk thresholds/gradients. Further research in this direction can thereby determine whether the avoidance responses generated depend on the degree of contamination-risk, the intensity of the cue presented and/or the severity of the threat implied. Such research can help us determine whether both behavioural and physiological responses are conserved across taxa, or whether some may have evolved during the course of primate evolution.

Ethics. All experimental procedures were approved by the Animal Welfare and Animal Care Committee of the Kyoto University Primate Research Institute (#2016-138).

Data accessibility. Supporting data are accessible in electronic supplementary material.

Authors' contributions. C.S. and A.J.J.M. designed the study; C.S. collected and analysed the data; R.B. supported data collection at Lola ya Bonobo Sanctuary; C.S. and A.J.J.M. wrote the manuscript; and all co-authors approved the final manuscript.

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