



Fear of missing out? Personality and plasticity in food neophilia by wild vervet monkeys, *Chlorocebus pygerythrus*

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ARTICLE INFO

Article history:

Received 17 November 2021

Initial acceptance 31 January 2022

Final acceptance 30 May 2022

Available online 4 August 2022

MS. number: A21-00648R

Keywords:

behaviouralreaction norm

Chlorocebus pygerythrus

food neophilia

personality

plasticity

social context

Animals often differ in their responses towards novelty, and sometimes these differences are consistent across individuals. Here, we explored interindividual variation in neophilia towards novel foods by recording whether animals ingested novel food stuffs ($N_{\text{individuals}} = 116$; $N_{\text{trials}} = 276$) in three troops of wild vervet monkeys. We tested for the effects of individual level variables, between-individual variation (i.e. personality), within-individual variation (i.e. plasticity) and variation in testing conditions (e.g. ecological conditions, proximate social environment). We found that our animals showed consistent differences towards eating novel foods, with lower-ranking animals displaying a more neophilic response than higher-ranking animals, and that neophilia was socially facilitated. Social facilitation did not depend on whether the partner was foraging, the social association between the focal and their partner or relatedness, indicating that the mere presence of another increased the likelihood that animals would eat the novel food. We also found some evidence that animals responded differentially to variation in their proximate social environment, as some, but not all, animals were more likely to eat the novel food as the number of partners increased, whereas others were not. Our results underscore the importance of testing behaviour and cognition under natural conditions rather than always doing so under strictly controlled settings and controlling for possible confounding factors statistically rather than controlling the testing conditions themselves.

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Many researchers choose to investigate individual level variation in behaviour by developing specific tests designed to measure animals' responses to controlled, novel stimuli (e.g. in primates: [Błaszczuk, 2017](#); ungulates: [Kelly et al., 2020](#); birds: [Schaffer et al., 2021](#)). Devising and conducting such tests ([Réale et al., 2007](#)) offers all the benefits of controlled experimental designs, including confidence that the stimuli are novel to the animals, measurement accuracy and the ability to observe the entirety of the behaviour in question. As animal behaviour is contingent on the motor, perceptual and motivational aspects of the tasks that are used, tests are often designed to narrow possible sources of variation ([Morand-Ferron et al., 2016](#)). For example, testing isolated animals is commonplace in laboratory-based primate cognition research ([Cronin et al., 2017](#)), which endeavours to minimize contextual (e.g. feeding motivation), ecological (e.g. food availability) and social

(e.g. social interaction) variability ([Morand-Ferron et al., 2016](#)). Similarly, field-based researchers have attempted to standardize testing environments by, for example, testing isolated animals, either by capturing them (e.g. house sparrows, *Passer domesticus*: [Vágási et al., 2021](#)), or by waiting until they are relatively isolated (e.g. for chacma baboons, *Papio ursinus*, ensuring conspecifics were more than 2.5 m away; see [Carter et al., 2013](#)).

Tightly controlled testing conditions may establish an environment that precludes variation in conditions that animals, especially those in the wild, experience (e.g. varying food availability), or which result in circumstances that are outside the range of the natural environment (e.g. isolating individuals in gregarious species; [Niemelä & Dingemans, 2014](#)). More recent work has, therefore, begun to challenge the ecological validity of such tests, given that the effect of ongoing environmental variation on cognition is itself a crucial area of research for animals that live in dynamic environments ([Cauchoix et al., 2020](#); [Cronin et al., 2017](#)). One solution is to account for possible confounding factors statistically, rather than by eliminating them from the testing conditions

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(Morand-Ferron et al., 2016). Such ‘realized cognitive ability’, (i.e. cognition assessed under natural conditions), offers a more accurate measure of the variability on which natural selection acts (Morand-Ferron et al., 2016; Niemelä & Dingemans, 2014). Furthermore, the possibility that behaviour may be influenced by the presence of conspecifics (i.e. an audience effect, see Zuberbühler, 2008 for an overview) cannot be explored if animals are tested in isolation. For example, Visalberghi and Frigaszy (1995) found that the social facilitation provided by the presence of conspecifics made capuchins (*Cebus apella*) more likely to investigate novel foods. Social facilitation has also been argued to facilitate the ontogeny of foraging (Galef, 1993) and social learning (Visalberghi & Frigaszy, 1995).

Ignoring context in studies of behavioural variation also neglects the possibility that consistent interindividual differences may arise in response to certain environmental variable(s), rather than being solely due to intrinsic differences in individuals’ behavioural responses. For example, Fairbanks (1996) found that the presence of a novel male gave rise to consistent interindividual differences in maternal protectiveness among captive vervet monkeys (i.e. some mothers were consistently more protective than others), in addition to plasticity in accordance with local social contingencies. In this study, therefore, we use the terminology of the ‘behavioural reaction norm’ (BRN) approach (Dingemans et al., 2010), which measures both within-individual variation across an environmental gradient (i.e. plasticity) as well as between-individual variation (i.e. personality). That is, we aimed to capture both how animals differ both in their average levels of a given behaviour and in how strongly they respond to variation in the environment.

More specifically, the aim of our study was to determine whether vervet monkeys exhibit personality and plasticity with respect to a measure of neophilia – whether animals would eat a novel food. This study formed part of a larger project aimed at understanding whether any such differences are associated with other behaviours, particularly social learning abilities (Nord, 2021). Although we initially attempted to test animals when no conspecifics were nearby (i.e. no other animals within 2 m), this proved difficult to achieve and was exceptionally time-consuming. We therefore decided that, rather than discard trials that included the presence of other animals, we would control statistically for variation in the proximate social environment in the following three ways: (1) by considering whether current or future focal animals were inadvertently exposed to the intended novel foods by a conspecific who was interacting with it; (2) by considering whether an ongoing trial was interrupted (i.e. whether a conspecific caused a focal animal to move away from the food item); and (3) by considering the effect of variables that accounted for variation in testing conditions and that were related to social interactions (e.g. local resource variability, novel food type). Furthermore, we also accounted for whether animals had been inadvertently exposed to the intended novel foods (i.e. if a conspecific interacted with the novel food during a trial that was focused on a different animal) or if they caused any other disruption to a trial alongside the other variables that accounted for variation in testing conditions (e.g. local resource variability, novel food type) in our models.

The first step in our analyses was to conduct several confirmatory tests to determine whether responses towards novel foods were similar to those shown in previous work on vervets, which examined responses to novel objects (Blaszczuk, 2017). We next conducted a series of exploratory analyses concerning the role of the proximate social environment on novel food neophilia alongside the tests for our direct predictions (Gelman, 2003).

Based on previous work investigating vervet monkey responses towards novel objects (Blaszczuk, 2017), we predicted that (1) vervets would vary in their propensity to eat novel foods (i.e. our

population would exhibit personality with regards to novel food neophilia). Given that Blaszczuk (2017) found no effect of the proximate social environment, we further predicted that (2) there would be no effect of social presence. Following Blaszczuk (2017), we also predicted that (3) juvenile males would be more neophilic than juvenile females, (4) juveniles would generally be more neophilic than adults and (5) there would be no effect of dominance rank on novel food neophilia. As these analyses revealed an effect of social presence, we went on to explore whether the conditions under which animals ate novel foods were dependent on their proximate social environment. Specifically, we asked whether novel food neophilia was (6) dependent on the behaviour of their partner; that is, whether the effect of social presence was dependent on either the mere presence of others (i.e. social facilitation) or on the foraging behaviour of partners (i.e. response facilitation) and/or (7) dependent on the social association history of the animals involved (e.g. whether animals that groomed each other more frequently were more likely to exhibit a social presence effect), or (8) dependent on the relatedness between the tested individual and any partner(s). We also explored whether (9) novel food neophilia varied in accordance with social context (i.e. was plastic); specifically, whether it was influenced by the number of conspecifics present during the trial. Finally, we accounted for variation in testing conditions as described above.

METHODS

Study Site, Subjects and Baseline Data Collection

We collected experimental data during two study periods (study period 1: January–May 2017; study period 2: March–May 2018) at the Samara Private Game Reserve, Eastern Cape, South Africa from three troops (‘PT’, ‘RST’ and ‘RBM’) of vervet monkeys that occupied adjacent and overlapping territories in semi-arid riparian woodland (Pasternak et al., 2013). All animals were uniquely identifiable from natural markings. Animals had no access to human food sources (e.g. rubbish bins) and had never been provisioned. They therefore did not associate observers with the presence of food. Group composition varied throughout the study period and details are given in Table 1. We have collected baseline data on these troops by one or more observers for 10 h each study day for at least 5 days per week since 2008 (RST, RBM) and 2012 (PT). Baseline data consisted of scan samples (Altmann, 1974) collected on all visible animals across a 10 min window every 30 min. We recorded the animal’s identity and behaviour (foraging, moving, resting, socializing) and the identity and distance of their nearest neighbours.

Aggressive interactions between all animals were recorded during baseline data collection using behaviour sampling (Martin et al., 1986; Nord et al., 2021). We included agonistic interactions

Table 1
Composition of study troops throughout the study period

Age/sex	Range	Mean
RST adult females	8–13	9
RST adult males	6–10	8
RST juvenile females	14–16	15
RST juvenile males	4–11	10
PT adult females	8–9	9
PT adult males	5–9	6
PT juvenile females	8–10	9
PT juvenile males	13–16	15
RBM adult females	5–10	7
RBM adult males	4–7	6
RBM juvenile females	14–16	15
RBM juvenile males	10–13	12

between all animals in the calculation of each troop's dominance hierarchy (see [Vilette et al., 2020](#)). For aggressive interactions, the identities of the aggressor (the animal that initiated the aggressive interaction) and the victim (the animal that received the aggressive interaction) were recorded. Aggressive interactions were defined as interactions during which one animal either performed a threat display (eye flash, vocal threat) towards another, or caused another to give up a resource (space, food, access to a conspecific) by approaching another (and sometimes coming into physical contact with them).

Experimental Data Collection: Novel Food Tests

To begin a novel food test, either C.N. or D.R. presented a novel food item to the focal animal (i.e. the animal being tested) by placing the item in the animal's path while it was either travelling or foraging. To do so, we turned our backs to the intended focal animal and placed the food item between our boots so as to block the item from view and prevent the possibility that animals could associate us with food. On occasion, we placed our backpacks on the ground to further block any view from the animals. In an effort to increase the food item's salience, we placed it on a bare piece of ground whenever possible, and we used artificial food colouring to dye five of the eight food items. Novel food items included 2 cm³ pieces of potato (blue or pink), marrow (yellow), eggplant (blue), green bean (red or undyed), pumpkin, baby corn, apple (pink) or sliced grapes. Any nonfocal animals that witnessed a focal animal engaging with a food item was subsequently tested using a different item in order to ensure novelty (e.g. [Fig. 1](#); however, see [Previous Exposure to the Food Item](#) below). Food tests were

repeated, using a new food type each trial, for as many animals as possible, both within and across field seasons (see [Supplementary material 1, Table S1](#) for a description of all trials across all focal animals). All trials were videorecorded using a Canon PowerShot ELPH 100 HS camera with observers standing at least 10 m away.

All video trials were coded in the laboratory by C.N. using Behavioural Observation Research Interactive Software (BORIS v.7.7.3; [Friard & Gamba, 2016](#)). We scored whether or not the novel food was eaten, defined as an individual bringing the food item into contact with its teeth. Animals were considered to be participants (i.e. 'focal animals') in the trial, and thus a trial began, if individuals clearly directed their gaze at the novel food for ≥ 1 s or walked within touching distance (dependent on the arm's length of each focal; ~ 15 – 25 cm) of the food item. If an animal only walked to within touching distance of the food item (relative to each animal) but did not gaze at or interact with it, the trial was coded as 'ignore'. Trials ended when either the focal ate the novel food or moved beyond 2 m of it. Animals that only gazed or ignored the food item were scored as not eating the novel food. Trials were excluded if the focal animal was within touching distance of the food item for less than 1 s (e.g. ran past it).

Inter-rater Reliability

All trials were filmed and coded post hoc by C.N. M.C., who was blind to experimental predictions, then coded a randomly selected ([Haahr, 2019](#)) subset of the trials (68 out of 281; 23.84%) in order to determine inter-rater reliability. We included all behaviours coded during the test in reliability calculations, including whether animals ignored the trial, looked at the novel food item, ate the novel



Figure 1. Animals during the novel food tests, demonstrating previous food item exposure (top), with no conspecifics nearby (bottom left) and social presence (bottom right).

food, how many partners were present and partner foraging behaviour. We calculated frequency within interval agreement (Miltenberger & Weil, 2013) and used the 'IRR' package (Gamer et al., 2019) in R to estimate Cohen's kappa.

Social Presence and Partner Foraging

Because any animal that walked to within touching distance of the food was considered a trial participant, multiple animals could be a focal animal in any given trial. We refer to any animal present during the trial that was not the focal as a 'partner' of the focal. We coded trials as 'social presence' if any partners(s) were present within 2 m of the focal animal before they ate the novel food or, if the focal animal did not eat the novel food, at any time during the trial. We also recorded the number of partners present. To determine whether the observed social presence effect (see Results) resulted from response facilitation, we recorded how many partners foraged, in general (on any available food item), before the focal ate the novel food ('partner foraging'). If the focal did not eat the novel food, we recorded how many partners foraged at all during the trial.

Although a previous study with vervets used a 1 m threshold for social presence (Blaszczuk, 2017), we have found 2 m to be a relevant social distance for our study groups (e.g. in a previous study, we found that males who had more spatial associations with females, recorded using a 2 m threshold, were more likely to improve their dominance rank; Young et al., 2017). Nevertheless, as the 2 m threshold may present an important difference between our study and previous work, we also conducted all analyses using a 1 m threshold and found qualitatively identical results (see Results, Supplementary material 1, Table S2). When we compared the models using different thresholds, we found that the model using 2 m received more support (i.e. had a higher theoretical expected log pointwise predictive density, 'ELPD'; see Results). We therefore present results using the 2 m threshold in the main text.

Affiliation Networks and Standard Ratio Index (SRI)

To determine a measure of social association between focal subjects and their partners that were present during the trial, we calculated a simple ratio index (SRI; Henzi et al., 2009) using the 'create.a.network' function in the 'netTS' package (Bonnell & Vilette, 2020) in R v.3.5.2 (R Core Team, 2018) for each animal present during the trial.

We calculated SRIs for each animal present during the trial using two affiliative networks, grooming and spatial proximity, constructed from the baseline data set. To determine an appropriate window size across which to construct the affiliative networks, we first identified the stability and robustness of each network by measuring dyad weights (i.e. ties) across 30-, 60-, 90- and 120-day time frames. We quantified network stability by determining whether the dyad weights converged within the time frame using the 'check.windowsize' function in the 'netTS' package (Bonnell & Vilette, 2020) in R. We quantified robustness by assessing the sensitivity of dyad weights to subsampling using the same function. These analyses revealed that a 90-day window size was the most appropriate to create all affiliative networks (see Supplementary material 1, Figs. S1, S2). Finally, because we were using these networks to test whether or not associations predicted behaviour during the novel food tests, we constructed each grooming and spatial proximity affiliative network using data from the 90 days prior to the date of the first trial on each troop for each study period.

We identified grooming dyads from instantaneous scan samples, yielding 4529 directed grooming samples in study period 1

($N_{RBM} = 1367$, $N_{RST} = 1255$, $N_{PT} = 1907$) and 2263 directed grooming samples in study period 2 ($N_{RBM} = 834$, $N_{RST} = 729$, $N_{PT} = 700$). Spatial proximity dyads were also collected from instantaneous scan samples, yielding 35 946 directed spatial proximity dyads in study period 1 ($N_{RBM} = 12 550$, $N_{RST} = 8540$, $N_{PT} = 14 856$) and 30 103 directed spatial proximity samples in study period 2 ($N_{RBM} = 11 129$, $N_{RST} = 7386$, $N_{PT} = 11 588$).

We calculated the SRI between each possible pair present – that is, if a focal had two partners ('A' and 'B'), we calculated the SRI between the focal and partner A, the focal and partner B, and between partners A and B, resulting in three values. We then calculated the mean SRI value for the group present during the trial. This allowed us to use a measure of social association for all animals within their specific social context during the trial.

Previous Exposure to the Food Item

If focal animals were tested with a food item they had witnessed previously (i.e. they had seen another animal interacting with this food type or they had seen it during one of their previous trials by mistake), we recorded the trial as 'food item exposed'.

Trial Interruption

Trials were recorded as 'trial interrupted' if a nonfocal animal physically contacted the focal animal and/or food item once the trial had begun but before the focal ate the food item, or if the focal animal and nonfocal animal engaged in aggression (see Dominance Rankings below for definitions of aggressive interactions) during the trial.

Age

Subjects were categorized as either juvenile or adult in relation to sexual maturity (~3.5+ years for females, 5+ years for males; see Jarrett et al., 2018).

Relatedness

The identity of mothers, their offspring and maternal siblings have been collected since 2011 as part of the Samara Vervet Monkey Project's ongoing baseline data collection. We therefore scored animals as related if they were either mother and offspring or maternal siblings.

Dominance Rankings

Dominance hierarchies were determined from decided, dyadic aggressive interactions ($N_{RBM} = 5061$; $N_{RST} = 5914$; $N_{PT} = 5619$) using the baseline data set for all troop members. Individual dominance ranks were estimated using the Elo-rating method and the 'EloRating' package (Albers & de Vries, 2001; Neumann et al., 2011; Vilette et al., 2020) in R using a 5-month burn-in period. We updated each animal's dominance ranking on the date of their test given that previous research has shown that rank is dynamic during this period (Nord et al., 2021). Dominance rankings of animals included in the current study were representative of the population overall (Supplementary material 1, Fig. S3).

Troop Level Estimates of Resource Availability

We used the normalized difference vegetation index (NDVI) to model differential resource availability experienced by the three troops, as this has been shown to be a strong correlate of food availability to wild vervets (Willems et al., 2009). NDVI estimates

were obtained using MODIS NDVI data downloaded from NASA's 'Reverb|ECHO' site (Didan, 2015). The Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM-1) collect MODIS data with a return-to-site periodicity of 16 days (Didan, 2015). We then used 'ArcGIS' v.10.6.1 to overlay the MODIS data onto troop territories, with each territory represented as a regular series of points 10 m apart. NDVI values were then extracted from the MODIS rasters at each point. Area-weighted averages for each territory were generated every 16 days since the project began in 2008 by averaging all NDVI values for points falling within the territory's 95% isopleth and weighted by the troop's differential usage of its territory during each 16-day period. During the study period, area-weighted NDVI values ranged from 0.28 to 0.62 (moderate values representing grasslands and shrubs; United States Geological Survey, 2018) and averaged 0.452 across the three troops.

Statistical Analyses

With the exception of Cohen's kappa for which no Bayesian equivalent is available, all analyses were conducted within a Bayesian framework. We constructed multilevel regression models (Gelman & Shalizi, 2012) using the package 'brms' in R. Sample sizes varied across the two models as the identities of some partners were unknown (5 of 276 trials).

All \hat{R} s = 1.0, confirming model convergence (Gelman & Shirley, 2011). We used the 'pairs' function in R to visually assess the presence of collinearity between variables in all models and found none. We determined model performance using the 'posterior predictive check' (pp_check) function of 'brms' and performed model comparisons using 'leave-one-out-cross-validation' ('LOO'; Vehtari et al., 2017) using the 'loo_compare' function of 'brms'. For model comparisons, we determined which model received the highest theoretical expected log pointwise predictive density ('ELPD'). All graphical outputs were created using the 'ggridge' (Wilke, 2020) and 'ggplot2' (Wickham, 2016) packages in R using the 'nord' (Kaupp, 2019) colour palette, and we specify 95% credible intervals (CI) in tables and plots.

Probabilities of eating novel foods and consistent interindividual differences to eating novel foods

We first determined if individuals differed in whether they ate novel foods. Specifically, we used a multilevel Bernoulli model (Model 1) to estimate the probabilities of animals eating the novel foods. We specified whether the focal animal ate the novel food (Yes/No) as the response variable and included social presence (Y/N; prediction 2), age/sex class (predictions 3 and 4), and dominance rank (prediction 5) as predictor variables. We included within-individual trial number (median = 3, range 1–6), food item type and NDVI as statistical controls for the possible effects of repeated experience with the testing condition, effects of food item type and variation in local ecological conditions, respectively. We also included previous food item exposure (Y/N) and trial interruption (Y/N) as statistical controls for animals that had been previously exposed to the tested food item and/or interrupted during the trial. Finally, we entered troop identity (ID), study period, observation and focal animal ID as group level effects. For this model, we specified four chains and 1500 iterations and included weakly informative priors (mean = 0, SD = 1).

We considered interindividual differences in whether animals ate novel foods (prediction 1) by analysing the amount of variance that animal identity and troop identity explained in Model 1. For this model, we specified four chains, 3000 iterations and weakly informative priors (mean = 0, SD = 1) on the model intercept and predictor variables. We could not calculate repeatability, a widely used measure of the behavioural variation in a population that is

due to differences between individuals (Nakagawa & Schielzeth, 2010) and which serves as a validity measure for tests of personality (Carter et al., 2012), because repeatability measures require an estimate of residual variance, and there is no direct way to estimate residuals from logistic regressions (Nakagawa & Schielzeth, 2010). Furthermore, in models with random slopes, repeatability is not uniquely defined as it depends on the coefficient(s) for which the random slope is applied.

Response facilitation, social association, relatedness and plasticity

To determine whether the social presence effect (see Results) constituted response facilitation and whether it was dependent on social association and/or relatedness, we constructed an additional Bayesian multilevel Bernoulli model (Model 2) using the same framework, response variable, predictor variables and grouping variables as Model 1 above, with a few alterations. For Model 2, we used the count of known partners rather than total partner count, because, unlike Model 1, Model 2 required animal identity in order to determine social association and relatedness. For five trials, the identity of one or more partners was unknown, and thus these trials were omitted from Model 2. Thus, we included the following as predictor variables in Model 2: (1) our measure of partner foraging, in order to determine whether the social presence effect was either social or response facilitated (question 6); (2) our grooming SRI, spatial proximity SRI and relatedness variables to determine whether the social presence effect was dependent on prior association (question 7) and/or relatedness (question 8) between the focal and its partner(s); (3) the count of known partners, in order to determine whether novel food neophilia was plastic in accordance with the proximate social environment (question 9). We also included random slopes to allow for interactions between predictor variables and random effects (i.e. allowing estimate slopes to vary by random effect level; Dingemanse & Dochtermann, 2013; Gelman & Hill, 2007), thus enabling us to capture individual plasticity in novel food neophilia under different social contexts. Specifically, to investigate plasticity, we included random slopes for each predictor variable for which animal ID could vary (i.e. food item exposure, trial interruption, food item type, dominance ranking, NDVI, count of known partners, partner foraging, SRI, relatedness) in an effort to increase model generalizability (Barr et al., 2013). We then compared the performance of Model 2 (with random slopes) to Model 1 (without random slopes) in order to investigate the amount of variance that animal identity and troop identity explained with respect to each random slope. For this model (Model 2), we specified four chains, 1500 iterations and weakly informative priors (mean = 0, SD = 1) on its intercept and predictor variables.

The social presence effects we found in Model 1 were not as clear in Model 2 (credible intervals were wider compared to our model without social association measures and random slopes; see Results). We suspected that this may have been due to our limited observations of more than two partners during a trial (e.g. of our 271 observations, only 16 included three or more partners). To test the possibility that our results were largely dependent on sample size, we constructed a random slope model with slightly more informative priors compared to Model 2 (using a Student's *t* distribution, mean = 0, SD = 1, *df* = 3), which allowed us to determine how sensitive our model was to prior choices (Gelman et al., 2017): models with small sample sizes are more sensitive (Diaconis & Freedman, 1986a, 1986b). We also compared this model to Model 2 with weakly informative priors.

Ethical Note

All protocols were noninvasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved

by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505). This study also adhered to the ASAB/ABS Guidelines for the use of animals in research.

RESULTS

A summary of the predictions made, the variables included and the results are given in Table 2. In total, we conducted 276 trials with 116 different animals (Table 3, Fig. 2); 104 trials were conducted where at least one partner was present. Partner count ranged from 0 and 4 (median = 0) across trials. We achieved an agreement of 91.1% for inter-rater reliability, and an unweighted Cohen's kappa of 0.719 ($z = 7.32$, $P < 0.001$).

Probabilities of Eating Novel Foods

We found that Model 1, which used 2 m as the threshold for social presence, received more support than the Model using 1 m (Supplementary material 1, Table S2; expected log pointwise predictive density 'ELPD' difference of the 1 m model = -0.48 , $SE = 1.14$). Responses towards food types varied, but we found no effect of within-individual trial number, NDVI, previous food item exposure or trial interruption for Model 1 (Table 4) or Model 2 (Table 5). We also found that probabilities varied regarding troop ID, trial ID, observer and study period for both Model 1 (Table 4) and Model 2 (Table 5); however, while the direction of these group level effects were clear, their magnitudes were uncertain, as indicated by the large range between the lower and upper 95% CI values.

We found that Model 2 received much higher support than Model 1 ($ELPD_{Model1} = -39.44$, $SE = 6.51$), but that Model 2 was

Table 3
Sample sizes of the novel food test trials

Age/sex	Participated	Ignored novel food	Ate novel food
Adult females	60 (25)	17 (9)	8 (3)
Adult males	31 (16)	20 (11)	0
Juvenile females	102 (38)	12 (6)	43 (15)
Juvenile males	83 (37)	5 (3)	28 (13)
Total	276 (116^a)	54 (29)	79 (31)

Parenthetical values indicate the total number of unique animals, as animals were tested multiple times.

^a Some animals aged up during the study period and are represented in the relevant age/sex class to which they belonged at the time of their trials. $N_{individuals} = 116$; $N_{trials} = 276$.

less certain than Model 1, as seen in the larger ranges of the CIs (Table 5). Model 2 became even less certain with the use of slightly more informative priors (Supplementary material 1, Table S3).

Do Animals Consistently Differ in Whether They Eat a Novel Food?

From Model 1, we found that eating novel foods varied consistently by animal ID, indicating consistent interindividual differences, and thus personality, in novel food neophilia (Table 4, Fig. 3).

Does Novel Food Neophilia Depend on Age, Sex or Dominance Ranking?

Using Model 1, we found that adult males were less likely to eat the novel foods overall, but there were no differences among adult females, juvenile females and juvenile males (Fig. 4). We also found

Table 2
Summary of the predictions made, variables included and results

Prediction/question	Type of analysis	Variable of interest	Model	Result
(1) Animals vary in their probability of eating a novel food	Confirmatory	Random intercept of animal ID	Model 1	There were consistent interindividual differences in the probability that animals ate novel foods (Table 4, Fig. 3)
(2) Novel food neophilia is not dependent on the proximate social environment	Confirmatory	Partner presence (Y/N)	Model 1	Animals were more likely to be novel food neophilic in the presence of a partner/partners (Table 4, Fig. 6)
(3) Juveniles are more novel food neophilic compared to adults	Confirmatory	Age/sex	Model 1	Juveniles were more likely to be neophilic compared to adults (Table 4, Fig. 4)
(4) Juvenile males will be more novel food neophilic compared to juvenile females	Confirmatory	Age/sex	Model 1	There were no clear differences in novel food neophilia across juvenile sex (Table 4, Fig. 4)
(5) Novel food neophilia does not vary by dominance rank	Confirmatory	Dominance rank	Model 1	Lower-ranking animals were more novel food neophilic compared to high-ranking animals (Table 4, Fig. 5)
(6) Is the social presence effect due to response facilitation?	Exploratory	Count of partners foraging	Model 2	Novel food neophilia did not depend on whether the partner was foraging; thus, novel food neophilia was socially facilitated (Table 5, Fig. 7)
(7) Is the social presence effect dependent on social association?	Exploratory	Grooming and spatial proximity SRI	Model 2	Novel food neophilia did not depend on social association (Table 5)
(8) Is the social presence effect dependent on relatedness?	Exploratory	Count of related partners	Model 2	Novel food neophilia did not depend on relatedness (Table 5)
(9) Is novel food neophilia plastic in accordance with the proximate social environment?	Exploratory	Random slope of partner count	Model 2	Novel food neophilia was plastic for some animals but not for others (Table 5, Fig. 8)

SRI = simple ratio index. Both models included the same response variable (whether or not the animal ate the novel food), covariates (normalized difference vegetation index, 'NDVI', trial interruption, previous food item exposure, food item type and within-individual trial number) and grouping variables (trial identity, animal identity, troop identity, study period and observer identity). Model 2 included random slopes on each grouping variable.

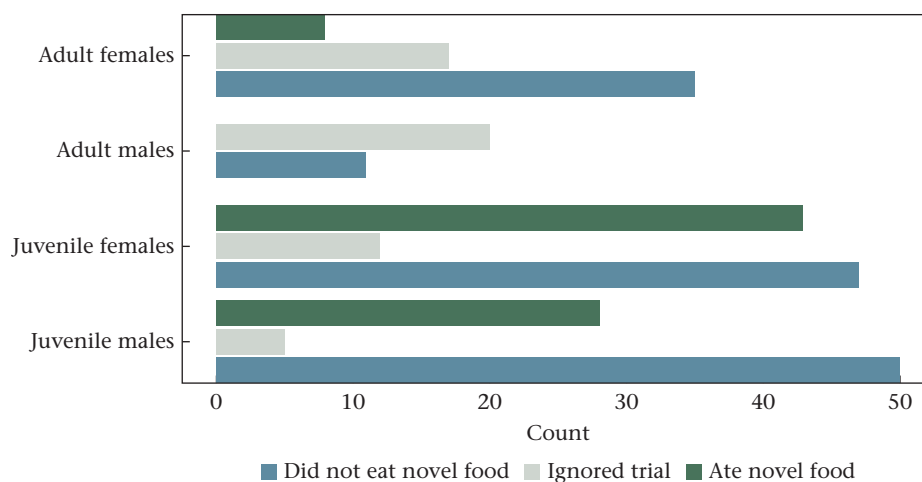


Figure 2. Trial outcomes by age/sex class. $N_{\text{trials}} = 273$.

Table 4

Posterior estimates of animals eating the novel food

Effect	Parameter	Estimate	Est. error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept (adult female, food: baby corn)	−2.183	1.354	−4.796	0.374
	Food item exposed (Y/N)	0.071	0.533	−0.965	1.163
	Trial interruption (Y/N)	0.296	0.516	−0.690	1.380
	Food: eggplant, blue	−0.992	0.773	−2.495	0.524
	Food: green bean	0.211	0.751	−1.245	1.696
	Food: green apple	−0.104	0.971	−1.966	1.734
	Food: potato, pink	−0.684	0.641	−1.996	0.543
	Food: pumpkin	−0.874	0.642	−2.113	0.390
	Food: red grape	1.265	0.712	−0.119	2.652
	Food: green bean, red	−0.063	0.909	−1.867	1.756
	Food: marrow, yellow	−0.011	0.661	−1.314	1.239
	Food: potato, blue	0.376	0.602	−0.837	1.548
	Social presence (Y/N)	1.914	0.499	0.934	2.940
	Adult males	−0.793	0.870	−2.530	0.888
	Juvenile females	0.899	0.640	−0.346	2.136
	Juvenile males	0.821	0.640	−0.437	2.094
	Within-individual trial number	0.122	0.289	−0.430	0.707
	Dominance rank	−0.836	0.408	−1.694	−0.135
	NDVI	0.306	0.478	−0.626	1.322
	Group level effects	SD(collector)	1.148	1.021	0.042
SD(study period)		1.439	1.354	0.048	5.034
SD(ID)		2.113	0.616	1.074	3.535
SD(troop)		1.603	1.177	0.202	4.626
SD(trial ID)		0.632	0.485	0.028	1.826

NDVI = normalized difference vegetation index. Age/sex is relative to adult females, food type is relative to baby corn. Estimates are on the logit scale; CI = credible interval; SD = standard deviation; $N = 276$; LOO-adjusted $R^2 = 0.282$ (lower 95% CI: 0.166; upper 95% CI: 0.385).

that lower-ranking animals were more likely to eat the novel food compared to higher-ranking animals (Table 4, Fig. 5).

Does Novel Food Neophilia Depend on the Proximate Social Environment?

Animals were more likely to eat the novel food if there was a partner present within 2 m during the trial (Model 1, Table 4, Fig. 6).

Is the Social Presence Effect Dependent on Response Facilitation, Social Association or Relatedness?

Model 2 found no evidence of a response facilitation effect – animals were no more likely to eat the novel food if their partners were foraging during the trial (Table 5, Fig. 7). Thus, the social presence effect was socially facilitated in that the mere presence of a conspecific, but not the conspecific's behaviour, increased novel

food neophilia. There was also no evidence that eating a novel food depended on social association or relatedness (Table 5).

Is Novel Food Neophilia Plastic?

There was evidence in Model 2 for individual level plasticity in novel food neophilia to be dependent on social context, but this effect was uncertain (Fig. 8). Additionally, the extent to which neophilia was plastic varied across animals. That is, some animals, across age and sex classes, were more likely to eat the novel food as their number of partners increased, while others were not (Table 5, Fig. 8).

DISCUSSION

We found that the vervets in our study groups displayed consistent interindividual differences in novel food neophilia and

Table 5
Posterior estimates of animals eating the novel food with partner foraging, association and random slopes

Effect	Parameter	Estimate	Est. error	Lower 95% CI	Upper 95% CI	
Population level effects	Intercept (adult female, food: baby corn)	−2.440	2.267	−6.861	1.990	
	Food item exposed (Y/N)	0.043	0.889	−1.743	1.818	
	Trial interruption (Y/N)	−0.030	0.963	−1.913	1.867	
	Food: eggplant, blue	−0.359	0.968	−2.228	1.531	
	Food: green bean	0.108	0.965	−1.777	1.990	
	Food: green apple	−0.050	0.991	−1.964	1.853	
	Food: potato, pink	−0.257	0.938	−2.114	1.562	
	Food: pumpkin	−0.389	0.956	−2.244	1.505	
	Food: red grape	0.731	0.989	−1.207	2.702	
	Food: green bean, red	0.000	0.995	−1.985	1.988	
	Food: marrow, yellow	−0.022	0.920	−1.828	1.767	
	Food: potato, blue	0.059	0.968	−1.842	1.943	
	Known partner count (social presence)	1.283	1.005	−0.756	3.189	
	Adult males	−0.451	0.977	−2.385	1.452	
	Juvenile females	0.496	0.879	−1.268	2.189	
	Juvenile males	0.818	0.885	−0.949	2.512	
	Within-individual trial number	0.209	0.604	−0.964	1.449	
	Dominance rank	−1.066	0.981	−2.897	0.970	
	NDVI	0.091	0.861	−1.578	1.765	
	Count partners foraging	0.129	0.901	−1.610	1.892	
	Grooming SRI	0.243	0.883	−1.494	1.983	
	Spatial proximity SRI	−0.082	0.873	−1.800	1.653	
	Count-related partners	0.392	0.991	−1.548	2.334	
	Group level effects	SD (collector)	2.326	2.120	0.088	7.652
		SD (study period)	3.063	2.697	0.105	9.742
		SD (troop)	2.661	2.355	0.115	8.411
SD (trial ID)		1.127	0.917	0.045	3.449	
SD (ID)		3.194	1.754	0.286	7.033	
ID slope (known partner count)		1.840	1.563	0.066	5.792	
Correlations	ID intercept slope	0.041	0.222	−0.402	0.473	

NDVI = normalized difference vegetation index. Age–sex is relative to adult females, food type is relative to baby corn. Estimates are on the logit scale; CI = credible interval; SD = standard deviation; SRI = simple ratio index; $N = 271$; LOO-adjusted $R^2 = 0.569$ (lower 95% CI: 0.486; upper 95% CI: 0.642). Slopes for all predictors, and correlations, are included in [Supplementary material 1, Table S4](#).

that lower-ranking animals were more likely to eat novel foods compared to higher-ranking animals. We also found that novel food neophilia was socially facilitated, but not response facilitated.

Our findings with respect to rank differ from previous work on vervets that investigated their latency to approach novel items, where no effects of rank were found (Blaszczuk, 2017). Our results are in line, however, with previous work suggesting that higher-ranking animals should be more neophobic, given their better access to resources and thus their lower potential payoffs (i.e. discovering a new food source) from approaching novel items compared to lower-ranking animals (Wolf et al., 2007; e.g. in birds: Greenberg, 2003; fish: Laland & Reader, 1999; but see Amici et al., 2020; Drea, 1998).

Many trials were conducted with partners present, which was not surprising given that vervets are highly social and the study animals were likely to be in the close vicinity of other members of their group (2–3 m on average). Unlike Blaszczuk (2017), who found no effect of social context when a partner was present for vervets tested with novel objects, we found that novel food neophilia increased with both social presence and for some animals more than others, as the number of partners increased. However, while novel food neophilia was socially facilitated – in that the presence of partners during the trial increased novel food neophilia – this was not dependent on whether partners were also foraging themselves; that is, there was no response facilitation effect. Furthermore, we found that social facilitation was not dependent on either social association or relatedness, indicating that the mere presence of another animal was enough to increase the likelihood that a target animal ate the novel food. It is possible that the presence of others prompted animals to eat the novel food in order to avoid displacement scrounging (i.e. when higher-ranking animals displace lower-ranking animals in order to gain access to a

food resource; Li et al., 2021), especially given that lower-ranking animals were more neophilic than higher-ranking animals. Indeed, these findings are akin to what is popularly referred to as ‘fear of missing out’ (FOMO) – animals were more likely to eat the novel foods when others were present, possibly to avoid losing the food item altogether. Finally, we also found that animals responded differently to variation in their proximate social environment, as some animals were more likely to eat the novel food as the number of partners increased, whereas others were not. However, these results were less certain, likely due to our limited sample size.

Taken together, these findings highlight several issues relevant to the study of cognition and personality, including behaviours like social learning. First, the fact that novel food neophilia changed with social context would never have come to light had we been successful in testing animals when no conspecifics were nearby, as is standard for novelty tests. We also found that neither being exposed to the food item before the trial, nor being interrupted during the trial, had any effect on whether animals ate novel foods. Given this, it is unclear why there is a preference to test animals singly, except in studies with small sample sizes that prioritize greater experimental control over the cost of housing and caring for many animals. In previous work, animals have been tested in isolation because researchers are often interested in personality as unexplained variance in a particular behaviour that is consistent across situations and time, thus accounting for any bias due to plasticity in relation to social influences. For example, in an experiment investigating parental care in house sparrows, Westneat et al. (2011) argued that true personality can only be measured once all potential sources of plasticity are controlled for, such that personality represents consistent interindividual differences that are intrinsic to each animal. However, as we have shown, current analytical approaches are increasingly capable of

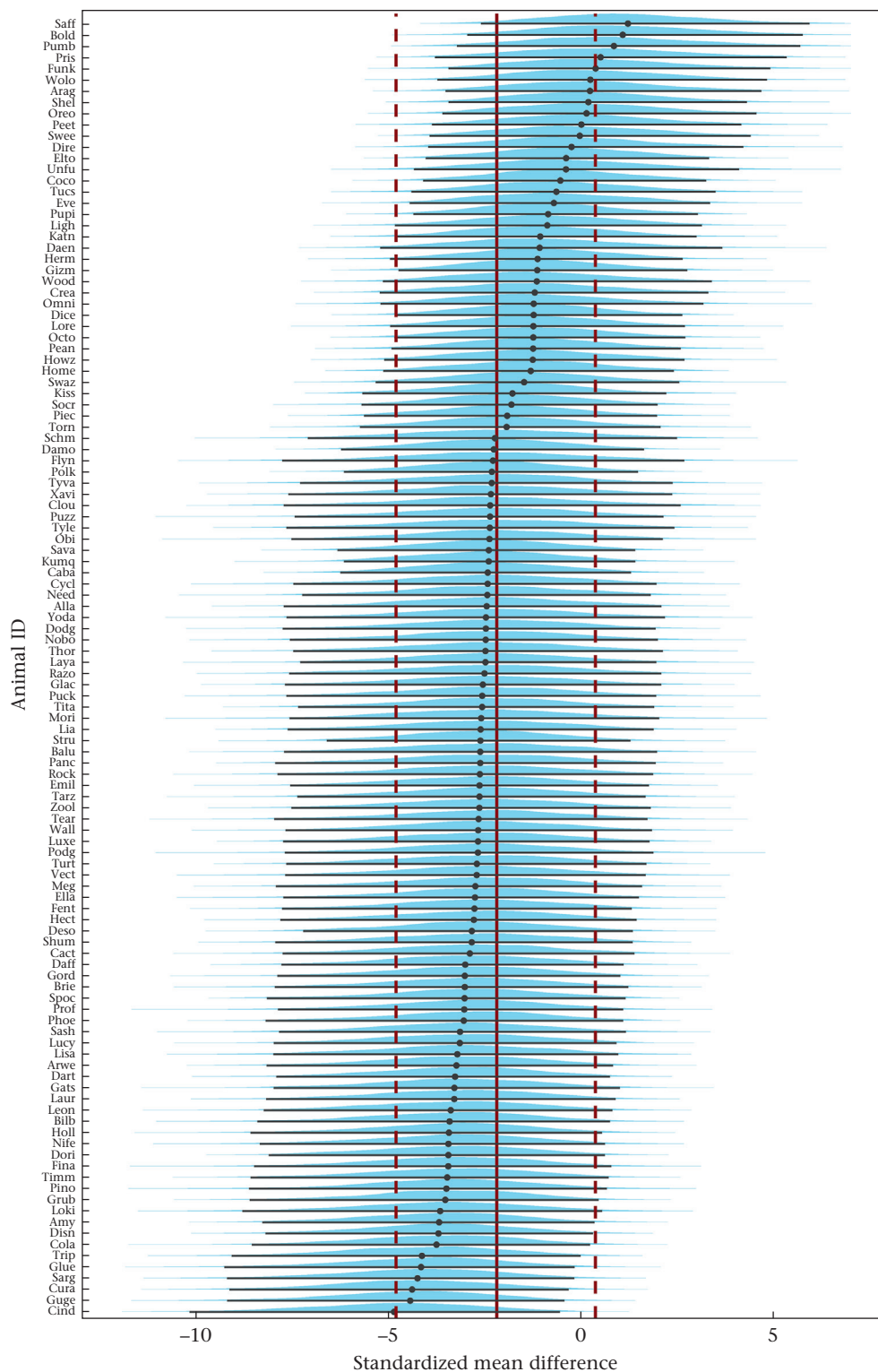


Figure 3. Standardized difference from the population mean in whether animals ate novel foods (Model 1). The solid red line indicates the population mean, and the dotted red line indicates the 95% credible intervals. Blue density curves represent the range of estimates predicted by the model for each animal, with the height of the density curve (and the black dot) indicating the likelihood of the estimate, and the spread of the curve indicating its uncertainty. $N_{\text{trials}} = 276$, $N_{\text{individuals}} = 116$ (Table 4); LOO-adjusted $R^2 = 0.285$ (lower 95% CI: 0.172; upper 95% CI: 0.384).

incorporating multiple confounding factors (i.e. variation in testing conditions) simultaneously, reducing the need to standardize the testing conditions themselves.

Galhardo et al. (2012), studying cichlid fish, have also questioned why animals, especially gregarious species, are tested in

isolation, given that their responses in such situations may not reflect those given in more naturalistic social settings. This is especially relevant for social learning, as familiarity with conspecifics can promote its occurrence (Swaney et al., 2001). Indeed, Greenberg (2003) specifically emphasized the importance of

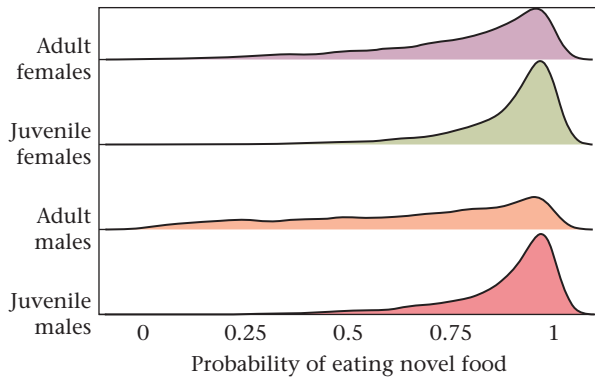


Figure 4. Probabilities of animals eating the novel food by age/sex from Model 1. Density plots present the range of probabilities predicted by the model, with the height of the density curve indicating the probability, and the spread of the curve indicating its uncertainty (Table 4). Probabilities are backtransformed from the logit scale into a probability scale.

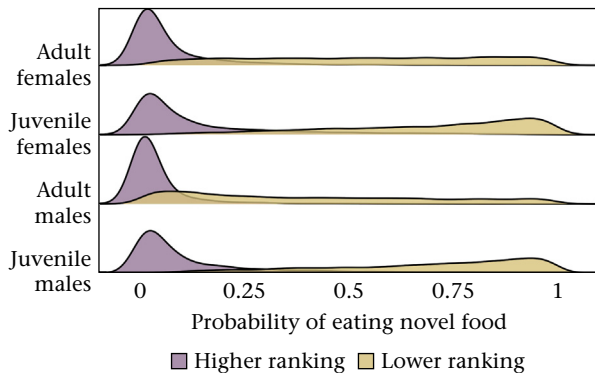


Figure 5. Probabilities of animals eating the novel food in accordance with their dominance ranking from Model 1. Density plots present the range of probabilities predicted by the model, with the height of the density curve indicating the probability, and the spread of the curve indicating its uncertainty (Table 4). Probabilities are backtransformed from the logit scale into a probability scale.

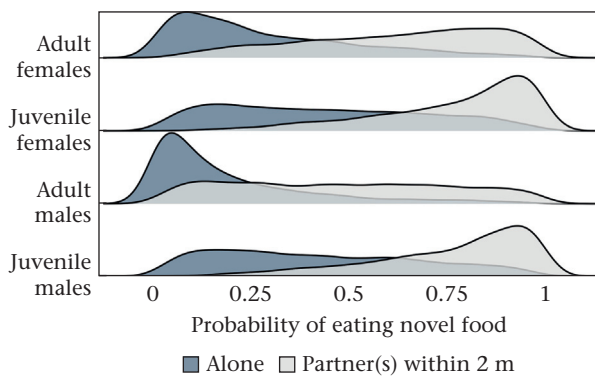


Figure 6. Probabilities of animals eating the novel food given the proximate social environment during the food trial from Model 1. Density plots present the range of probabilities predicted by the model, with the height of the density curve indicating the probability, and the magnitude of the effect and the spread of the curve indicating its uncertainty (Table 4). Probabilities are backtransformed from the logit scale into a probability scale.

understanding neophilia in relation to the spread of innovations, i.e. social transmission. For innovation to occur, animals must be willing to approach novel objects and situations, and this attraction must spread for social transmission of the innovation to take place.

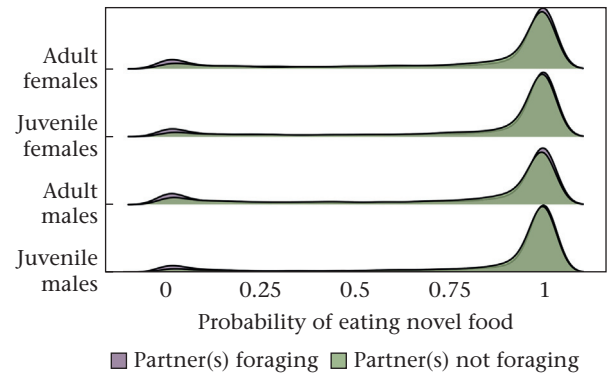


Figure 7. Probabilities of animals eating the novel food dependent on the partner foraging or not foraging during the food trial from Model 2. Density plots present the range of probabilities predicted by the model, with the height of the density curve indicating the probability and the magnitude of the effect and the spread of the curve indicating its uncertainty (Table 5). Probabilities are backtransformed from the logit scale into a probability scale.

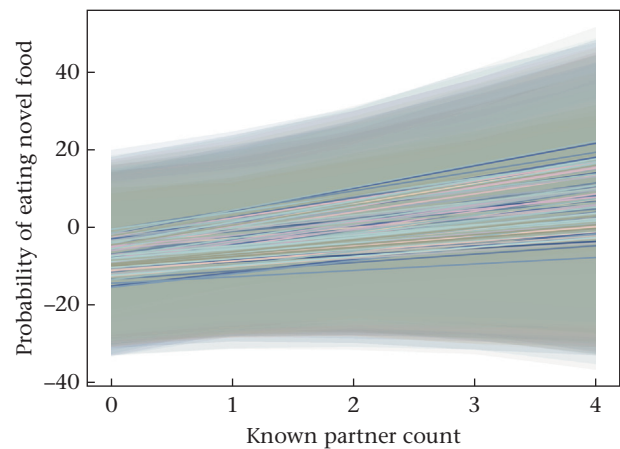


Figure 8. Model predictions of individual level reaction norms representing the probability of eating the novel food as a function of known partner counts from Model 2. Estimates are on the linear scale (Table 5).

Thus, attending to others who are more neophilic can relax the need for individuals themselves to be exploratory, and, ‘by influencing the propensity to approach novel situations, social responses to novelty become a critical feature in the development of innovative [behaviour]’ (Greenberg, 2003, p. 179).

Given these considerations, along with our finding that neither previous food type exposure nor trial interruptions had any effect on subsequent behaviour, the concern that variation in testing conditions may influence or obscure measures of personality and/or responses to novelty may be misplaced. The multilevel modelling approach used here not only accounted for trial interruptions, as well as previous food item exposure, but also revealed a social facilitation effect that could have important implications for personality and cognition research. This might otherwise have gone undocumented had we been able to run our trials as planned. In addition, our Bayesian approach allowed us to demonstrate that there was no effect of interruption (i.e. we found evidence of the absence of an effect, rather than showing only absence of evidence) or previous exposure to the novel food, while providing positive evidence of social facilitation – i.e. this approach provides good statistical control over potentially confounding variables, and to some degree obviates the need for the strict experimental conditions deemed necessary to obtain reliable and valid personality scores.

We also found that many animals ignored the trials, coming to within 0.5 m of the intended novel food but not engaging in any behaviours towards it. We know that these animals are excellent at discriminating colourful objects, particularly at close range, so it seems unlikely that the animals failed to detect the presence of the novel food. Rather, it appears that some animals, particularly adults, may have actively avoided the novel food tests. Thus, although animals may not differ in novel food neophilia depending on their age and sex, they may differ in whether they ignore a trial altogether; this is an issue that awaits further exploration.

Finally, these findings speak to the advantages of adopting a BRN approach to investigations of individual differences in behaviour (Dingemanse et al., 2010), as we found that animals were not only consistent in eating novel foods but also showed plasticity in doing so dependent upon social context. The BRN approach, however, requires a considerable amount of data – researchers must measure individuals multiple times in multiple contexts. Our results, which were dependent on sample size, exemplify this: although we found that novel food neophilia was plastic, we were unable to estimate this plasticity with any certainty. That BRN analyses require large data sets may explain the paucity of behavioural reaction norm research, especially among wild primates. Although there is now an increasing number of studies that document primate personality (reviewed in Blaszczyk, 2019), there is still a lack of research into behavioural plasticity. This is unfortunate given that phenotypic plasticity is seen as a defining trait of the primate order.

In summary, these results demonstrate the importance of investigating how cognition may vary with the environment (i.e. be plastic) and the value of reporting such measures and conditions. As Cauchoix et al. (2020) have pointed out, this will enable more accurate measures of cognitive abilities and determine which aspects of behaviour are repeatable or plastic (Dingemanse et al., 2010).

Author Contributions

Christina M. Nord led the investigation, visualization and data curation. Delaney Roth and Madison Clarke contributed to the data curation. Louise Barrett and S. Peter Henzi led the supervision, funding acquisition, resources and project administration. Conceptualization was led by Christina M. Nord, Louise Barrett and S. Peter Henzi, and methodology was led by Christina M. Nord, Tyler R. Bonnell, Louise Barrett and S. Peter Henzi. Christina M. Nord, Tyler R. Bonnell and Marcus J. Dostie conducted the formal analysis, and Christina M. Nord, Tyler R. Bonnell, Louise Barrett and S. Peter Henzi devised the methodology and reviewed and edited the manuscript. The original draft of this manuscript was led by Christina M. Nord, Louise Barrett and S. Peter Henzi.

Acknowledgments

Funding for fieldwork was provided by National Research Foundation (NRF, South Africa) awards to S.P.H. and Natural Sciences and Engineering Research Council of Canada (NSERC) grants to S.P.H. and L.B. L.B. is also supported by NSERC's Canada Research Chairs Program (Tier 1). T.B. is supported by a Fonds de Recherche du Québec – Nature et Technologies (FRQNT, Canada) Postdoctoral Fellowship and the Canada Research Chairs program (L.B.). C.N. is supported by a Student Grant from the Animal Behavior Society. C.N. and M.D. received funding allocation from L.B.'s NSERC's Canada Research Chairs Program. We are grateful to Mark and Sarah Tompkins for permission to work at Samara Private Game Reserve. We are indebted to all students and research assistants that assisted with data collection and to Kitty and Richard Viljoen for general and

logistical support. The manuscript benefited from discussions with Jean-Baptiste Leca, as well as insights provided by two anonymous referees. An earlier version of these data as well as early interpretations were disseminated as a virtual presentation at the 2020 Animal Behavior Society Meeting.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anbehav.2022.07.002>.

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