TITLE: Variation in neophilia in seven primate species

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We have no known conflict of interest to disclose.

All data and analysis code have been made publicly available as Supplemental Material.

This study was not preregistered.

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ABSTRACT

Neophilia is a measure of individuals' attraction to novelty and is thought to provide important fitness benefits related to the acquisition of information and the ability to solve novel problems. Although neophilia is thought to vary across individuals and species, few studies have made direct comparisons to assess the factors that predict this variation. Here we operationalized neophilia as the probability of interacting with novel objects and compared the response to familiar and novel objects in 53 captive individuals belonging to 7 different primate species: chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus),* Sumatran orangutans (*Pongo abelii*), gorillas (*Gorilla gorilla*), long-tailed macaques (*Macaca fascicularis*), tufted capuchin monkeys (*Sapajus apella*) and Geoffroy's spider monkeys (*Ateles geoffroyi*). Our results showed that individuals were overall more likely to interact with novel than familiar objects. Moreover, we found no evidence that neophilia varied across individuals depending on their sex, age and dominance rank. However, macaques were overall less likely to interact with objects (regardless of their novelty), as compared to bonobos, orangutans, gorillas and capuchin monkeys.

INTRODUCTION

The term neophilia is often used in literature to refer to attraction to novelty, resulting in preferential manipulation of novel objects (Greenberg 2003; Greenberg & Mettke-Hofmann 2001; Griffin & Guez 2014). Whereas neophilia may expose individuals to new challenges and risks, it is also thought to provide important fitness benefits related to the acquisition of information about the environment (Griffin & Guez 2014; Menzel 2017; Renner 1990) that can be later used to deal with socio-ecological problems more effectively (Liquin & Gopnik 2022; Reader & Laland 2003; Russell 1983). For instance, neophilia may lead individuals to more likely interact with novel set-ups, not only increasing the probability that they will solve simple problems by chance, but also providing them with more opportunities to acquire relevant information about object properties, which may be used to solve novel problems (Byrne 2016; Greenberg 2003; Greenberg & Mettke-Hofmann 2001; van Schaik & Burkart 2011).

Neophilia can vary substantially within and between species, depending on the potential risks and benefits associated with it. First, neophilia may differ between sexes due to differences in their physiological demands and parental investment (Greenberg & Mettke-Hofmann 2001; Santillán-Doherty et al. 2010). In species where males invest less in their offspring than females, males are expected to engage in riskier behaviors to increase mating opportunities, and may also be more neophilic than females (Gagnon et al. 2016; Kappeler & van Schaik, 2002; Santillán-Doherty et al. 2010). Second, higher-ranking individuals usually have priority of access to resources and thus more energy, and may better cope with the risks associated to novelty, being

more neophilic than lower-ranking ones (Santillán-Doherty et al. 2010). Third, neophilia may

differ depending on the individual's age. For individuals who need to acquire a substantial

amount of information during early life, neophilia can provide crucial benefits, and younger

individuals may thus be more neophilic than older conspecifics (Bergman & Kitchen 2009;

Biondi et al. 2010; Martina et al. 2021). Finally, although direct across-species comparisons are

scant, dietary generalist species, feeding on a variety of different items, are expected to be more

neophilic than more specialist species (Forss et al. 2017; Greenberg & Mettke-Hofmann 2001;

but see Henke-von der Malsburg & Fichtel 2018).

In this study, we aimed to assess how neophilia varied across individuals and species in

captive primates. We tested 53 individuals belonging to 7 different species: chimpanzees (*Pan*

troglodytes), bonobos (*Pan paniscus*), Sumatran orangutans (*Pongo abelii*), gorillas (*Gorilla*

gorilla), long-tailed macaques (*Macaca fascicularis*), tufted capuchin monkeys (*Sapajus apella*)

and Geoffroy's spider monkeys (*Ateles geoffroyi*). Based on previous literature, we predicted that

males, younger and higher-ranking individuals would be more neophilic than females, older and

lower-ranking conspecifics (Prediction 1). Moreover, we predicted that species with a wider

dietary breadth (i.e., dietary generalists: orangutans, capuchin monkeys, gorillas and

chimpanzees; see supplementary information in MacLean et al. 2014) would be more neophilic

than other species (i.e., more specialist species: bonobos, spider monkeys and long-tailed

macaques; Prediction 2).

METHODS

Ethics. All procedures complied with the principles of ethical treatment established by the European Union and the German government. All the institutions and facilities hosting the study primates controlled and approved all the procedures. Experimental protocols were approved by the Wolfgang Koehler Primate Research Center in the Leipzig Zoo, Germany, and the methods were carried out in accordance with the relevant regulations and guidelines.

Subjects. We studied captive great apes and monkeys from 7 groups, each belonging to a different species (N=53). Subjects included 7 chimpanzees, 5 bonobos, 5 orangutans and 4 gorillas at the Wolfgang Koehler Primate Research Center in the Leipzig Zoo, Germany, 11 long-tailed macaques at the Research Group Behavioral Biology, University of Utrecht, Netherlands, 12 capuchin monkeys at the ISTC-CNR Primate Center in Rome, Italy, and 9 spider monkeys at the Centenario Zoo in Merida, Mexico. The study subjects had different sex (i.e., 32 females and 21 males), age (i.e., 35 adults and 18 juveniles/subadults; Kappeler & Pereira 2003; Smuts et al. 1987) and dominance rank (i.e., 19 higher-ranking individuals, 17 middle-ranking individuals, and 17 lower-ranking ones, as assessed by the experimenter shortly before the neophilia task based on priority of access to food). They were all born in captivity, except for one gorilla (Bebe) and spider monkeys, who were wild born. Spider monkeys had been captured

to become pets at different ages, and although their individual histories and previous rearing

conditions were not known in details, most of them had spent few months to several years tied

with a chain in yards in rural areas of Mexico, before being rescued and moved to the Centenario

Zoo.

All individuals were housed in social groups with their conspecifics, in enclosures that had

indoor and outdoor areas. They participated on a completely voluntary basis and were never food

or water deprived during the experiments. All subjects had experience being temporally isolated

in testing rooms by a familiar experimenter for non-invasive testing, although the extent of

exposure to experimental tests partially varied across individuals. In particular, previous

exposure to experimental test at the onset of our study was highest in chimpanzees and bonobos

(i.e., most individuals had participated in experimental tests at least on a weekly basis for several

years), lowest in spider monkeys and long-tailed macaques (i.e., individuals had participated in

experimental tests for several months, mostly with lower frequencies), and intermediate in

orangutans, gorillas and capuchin monkeys (i.e., most individuals had participated in

experimental tests for several years, but mostly with lower frequencies).

Experimental procedures. We collected data in 2006 on spider monkeys and 2007 on the

other species. We tested subjects individually in a room, with no other conspecific having visual

access to the subject. If mothers had a young offspring, the latter was also allowed in the room.

The task consisted of two 10-minute sessions administered on two different days, which we

video-recorded and subsequently scored. Over the two sessions, we used 4 different novel

objects for each subject, with objects differing in terms of color and material (e.g., a pink plastic

comb, black metal pincers, yellow plastic bottle, grey metal cheese-peeler). On the first day, we

placed three novel objects in the testing room before the subject entered it, whereas on the

second day, we placed two of the three objects used in the first session (i.e., familiar objects) and

a new object (i.e., novel object), counterbalancing across trials and subjects the objects that we

used. From the videos, we later scored whether subjects contacted each object with the limbs or

the head during either day.

Statistical analyses. We analyzed our data with a binomial generalized linear mixed model

in R, version 4.4.0 (R Core Team 2022), using the glmmTMB package (Brooks et al. 2017). Our

dataset included one line for each subject and object (i.e., two familiar and four novel objects)

used over the two sessions (N=318). We modeled whether the probability of interacting with

objects varied depending on the four 2-way interactions of novelty (i.e., whether the object was

familiar or novel) with species, age (i.e., adults or subadults/juveniles), sex (i.e., females or

males) and rank (i.e., low, middle or high). These interactions allowed us to assess whether,

depending on their species, age, sex and/or rank, individuals differed in their probability of

interacting with novel as compared to familiar objects. Moreover, we included all the main terms

of the interactions in the model, and subject and object identity as random intercepts. This model

was then compared to a null model only including random factors, using likelihood ratio tests

(Dobson & Barnett 2018). If the full-null model comparison was significant, we used the drop1

function to assess which predictors had a significant effect. If interactions were not significant,

we re-ran the model after removing them. If categorical predictors with more than two levels

were significant, we used the package emmeans to conduct posthoc tests with Tukey adjustments

(Lenth 2019). We checked model assumptions using the DHARMa (Hartig 2022) and the

performance packages (Lüdecke et al. 2021), and we detected no convergence, dispersion or

collinearity issues (maximum variance inflation factor = 2.07; Miles 2005). More complex

models (e.g., including the 3-way interactions of novelty and species with age, sex and rank), in

contrast, failed to converge and are not reported. Therefore, we report descriptive statistics about

the probability of interacting with familiar and novel objects for each species depending on sex,

age class and rank (Table 1).

   Transparency and openness. We did not perform prior analyses to determine our sample

size, but rather included all subjects that were available for testing at the study locations. We did

not exclude any data from the analyses, and we report all manipulations conducted during our

study. We followed JARS (Kazak 2018). The statistical analyses reported here are not the

original ones we conducted and have been improved as a response to the Reviewers' comments

to a previous version of this work. The script is available as Supplemental Material at [link]. This

study design and its analysis were not pre-registered.

RESULTS

Overall, all bonobos, gorillas and orangutans interacted with novel objects at least once, in contrast to 86% chimpanzees (i.e., 6/7), 75% capuchin monkeys (i.e. 9/12), 56% spider monkeys (i.e., 5/9) and 9% macaques (i.e., 1/11). All bonobos and gorillas also interacted with familiar objects at least once, in contrast to 80% orangutans (i.e., 4/5), 43% chimpanzees (i.e., 3/7), 50% capuchin monkeys (i.e., 6/12), 33% spider monkeys (i.e., 3/9) and 9% macaques (i.e., 1/11). In Table 1, we report the probability of interacting with familiar and novel objects for each species depending on individuals' sex, age and rank. In Table 2 we report the proportion of trials in which each individual interacted with novel and familiar objects at least once during the trial.

The full model significantly differed from the corresponding null model ($\chi^2(21) = 62.32$, $p < 0.001$). None of the interactions had a significant effect, suggesting no clear differences across species, age, sex and rank in individuals' probability of interacting with novel as compared to familiar objects. The probability of interacting with objects varied depending on species and novelty (Table 3). In particular, individuals were overall more likely to interact with novel than familiar objects ($p<0.007$), regardless of species. Post-hoc tests revealed that macaques were overall less likely to interact with objects as compared to bonobos ($p=0.001$), orangutans ($p=0.004$), gorillas ($p=0.005$) and capuchin monkeys ($p=0.030$; Figure 1), regardless of object novelty.

DISCUSSION

In this study we investigated how neophilia varied across individuals belonging to seven primate species. Our results showed that individuals were overall more likely to interact with novel than familiar objects, regardless of their species, sex, age and rank. These findings contrast with our prediction that species would differ based on their feeding ecology, but they are in line with findings that captive animals are often neophilic, possibly because they live in less risky and more predictable environments and/or have more experience with anthropogenic objects, as compared to wild conspecifics (e.g., Benson-Amram et al. 2013; Bergman & Kitchen 2009; Damerius et al. 2017; Huber & Gajdon 2006; Lazzaroni et al. 2019; van Schaik et al. 2016).

We found no evidence that neophilia varied across individuals depending on their sex, age and dominance rank, contrary to our Prediction 1 and to previous studies in other species (Bergman & Kitchen 2009; Biondi et al. 2010; Gagnon et al. 2016; Martina et al. 2021; Santillán-Doherty et al. 2010). There are at least four reasons for these findings. First, failure to detect inter-individual differences in our study might depend on our limited sample size. Second, it is possible that sex, age and rank affect neophilia, but differently across species, so that larger datasets and more complex models may be needed to detect these effects. However, we could not detect any such a pattern from the descriptive data in Table 1. Third, our subjects all lived in captive settings and shared largely similar environments (e.g. confined spaces, no predation risk,

food provision, extensive exposure to humans and human artifacts), and this might have partially masked potential inter-individual differences that could be instead present in wild conspecifics. However, this explanation is unlikely because some of the studies that found evidence of inter-individual differences were also conducted in captivity (e.g., Biondi et al., 2010; Santillán-Doherty et al. 2010). Fourth, as response to novelty has complex implications for individual fitness (Ferrari et al. 2015; Smith & Blumstein 2008), it is possible that different individuals may find different ways to balance costs and benefits of neophilia, regardless of their sex, age and rank (see Greenberg 2003). In the latter case, our findings would not be the spurious result of methodological limitations, but rather mirror the lack of a consistent pattern that can be simply explained by these variables.

Contrary to Prediction 2, we found no inter-specific differences in the probability of interacting with novel objects, although species differed in the probability of interacting with objects in general, regardless of their novelty. In particular, bonobos, orangutans, gorillas and capuchin monkeys were more likely to interact with objects than long-tailed macaques. These results contrast with a previous study that found inter-specific differences between bonobos, orangutans and chimpanzees in their reaction to novelty, with chimpanzees and orangutans approaching novel objects more quickly than bonobos (Herrmann et al. 2011). However, this is not surprising, as, Herrmann and colleagues (2011) operationalized response to novelty as the latency to approach novel objects, a measure that is often used for neophobia, which is generally considered a trait independent from neophilia (Greenberg 2003; Greenberg & Mettke-Hofmann

2001). Moreover, the two studies included mostly different individuals, so that inter-individual

differences in reaction to novelty might also explain these seemingly contrasting findings.

The inter-specific differences we found in the probability of interacting with objects can

hardly be explained by dietary breadth, because dietary breadth specifically predicts differences

in neophilia, rather than more generally in exploration. Species with a higher degree of extractive

foraging (i.e., bonobos, capuchin monkeys and chimpanzees) might be expected to more likely

interact with objects, regardless of their novelty, as extractive foraging and tool use require the

manipulation of objects (see Boinski et al. 2000; Day et al. 2003; Greenberg 2003). However,

our study found no evidence of differences between these three species and the other ones.

Finally, inter-specific differences in the probability of interacting with objects did not reflect

clear differences in individual histories or previous exposure to experimental tests and human

artifacts. Spider monkeys, for instance, were the only individuals that had been raised as pets,

whereas chimpanzees and bonobos included individuals with the highest exposure to

experimental tests. Nonetheless, both spider monkeys and chimpanzees (but not bonobos)

showed an intermediate level of exploration (Fig. 1). Similarly, exposure to experimental tests at

the onset of our study was lowest in macaques and spider monkeys, as both study groups had

participated in experimental tests for only several months. Yet, only macaques were less likely

than most other species to interact with objects (i.e., only one of the 11 macaques interacted with

objects, a middle-ranking, adult female), although all macaques were born and raised in captivity

and were routinely exposed to human artifacts in their enclosure.

There are several reasons why we might have failed to find support for Prediction 2. First, as for inter-individual differences, it is possible that our limited sample size of captive individuals was not representative enough and might have masked potential inter-specific differences that are instead present across wild groups. This is especially true if neophilia emerges as a response to the ecological challenges experienced by individuals during their ontogeny, rather than being a relatively fixed species-specific trait. Second, differences in dietary breadth across our study groups may not have been sufficiently wide, and the inclusion of species with larger differences in dietary breadth may provide different results (see MacLean et al. 2014). Third, there are several other socio-ecological factors that might predict variation in neophilia, which we did not include in our analysis, like predation levels, habitat risk, environmental variability, migration patterns and social learning opportunities (Forss et al. 2017; Mettke-Hofmann 2014; Sol et al. 2011). Specifically assessing the role of these multiple factors, by including species that vary along them, might thus provide different results.

In conclusion, we found that captive individuals belonging to seven primate species were more likely to interact with novel than familiar objects. We found no evidence that neophilia varied across individuals depending on their sex, age and dominance rank. Future studies could overcome the limitations inherent to our limited and highly heterogenous sample of captive groups by including more groups for each species, ideally living in different conditions. Such an improved sample would be essential to better contrast the different evolutionary hypotheses regarding the distribution of neophilia across primates. In addition, due to the fact that response

to novelty is a complex and multifactorial construct, future studies should collect additional

measures of response to novelty (e.g., neophobia, see Greggor et al. 2015) with multiple stimuli

(e.g., objects, food, agents) and consider additional factors (e.g., number of years in captivity,

previous experience with objects/human artefacts, early adverse experiences) that could

contribute to explain the response to novelty variation within and between species.

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TABLE 1. Mean ± SD probability of interacting with familiar (F) and novel (N) objects for each species, depending on the sex, age class and rank of the individuals (empty cells represent age classes or ranks for which no individuals were available for that species).

Species	Sex				Age class						Rank					
	Female		Male		Juvenile		Subadult		Adult		Low		Middle		High	
	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N
Bonobo	1.00±0.00	1.00±0.00	1.00±0.00	0.92±0.12					1.00±0.00	0.95±0.10	1.00±0.00	1.00±0.00	1.00±0.00	0.88±0.13	1.00±0.00	1.00±0.
Capuchin monkey	0.20±0.24	0.35±0.30	0.50±0.46	0.68±0.39	0.00±0.00	0.00±0.00	0.60±0.49	0.70±0.40	0.25±0.25	0.50±0.32	0.33±0.47	0.50±0.41	0.33±0.24	0.42±0.31	0.42±0.45	0.63±0.
Chimpanzee	0.30±0.40	0.40±0.34	0.50±0.50	0.50±0.00			1.00±0.00	0.50±0.00	0.25±0.38	0.42±0.31	0.50±0.41	0.42±0.12	1.00±0.00	1.00±0.00	0.00±0.00	0.25±0.
Gorilla	0.67±0.24	0.92±0.12	1.00±0.00	1.00±0.00	0.50±0.00	0.75±0.00			0.83±0.24	1.00±0.00	0.50±0.00	0.75±0.00	0.75±0.25	1.00±0.00	1.00±0.00	1.00±0.
Long-tailed macaque	0.07±0.17	0.07±0.17	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.10±0.20	0.10±0.20	0.00±0.00	0.00±0.00	0.17±0.24	0.17±0.24	0.00±0.00	0.00±0.
Orangutan	0.75±0.43	0.81±0.32	1.00±0.00	1.00±0.00					0.80±0.40	0.85±0.30			0.67±0.47	0.75±0.35	1.00±0.00	1.00±0.
Spider monkey	0.42±0.45	0.46±0.47	0.00±0.00	0.42±0.42			0.38±0.41	0.44±0.45	0.20±0.40	0.45±0.46	0.63±0.41	0.69±0.41	0.00±0.00	0.08±0.12	0.00±0.00	0.50±0.

TABLE 2. Subjects that participated in the task, with their species, sex, age, rank, and proportion of trials in which they interacted with familiar and novel objects at least once during the trial (out of the two trials with familiar objects they were exposed to and the four trials with novel objects).

Species	Subject	Sex	Age	Rank	Familiar	Novel
Chimpanzees	Corry	F	A	L	0	0.5
	Dorien	F	A	H	0	0
	Fraukje	F	A	M	1	1
	Lome	M	S/J	L	1	0.5
	Riet	F	A	H	0	0.3
	Robert	M	A	H	0	0.5
	Sandra	F	A	L	0.5	0.3
Bonobos	Joey	M	A	M	1	1
	Kuno	M	A	L	1	1
	Limbuko	M	A	M	1	0.8
	Ulindi	F	A	H	1	1
	Yasa	F	A	H	1	1
Orangutans	Bimbo	M	A	H	1	1
	Dokana	F	A	M	1	1
	Dunja	F	A	M	0	0.3
	Padana	F	A	M	1	1
	Pini	F	A	H	1	1
Gorillas	Bebe	F	A	M	0.5	1
	Gorgo	M	A	H	1	1
	Kibara	F	S/J	L	0.5	0.8
	Viringika	F	A	M	1	1
Long-tailed macaques	Anastasia	F	S/J	L	0	0
	Cleo	M	A	H	0	0
	Era	F	A	H	0	0

	Icetea	F	A	M	0.5	0.5
	Logica	F	S/J	L	0	0
	Ofelia	F	S/J	L	0	0
	Salvadoro	M	S/J	L	0	0
	Sea	F	A	M	0	0
	Sumatra	F	A	M	0	0
	Video	M	S/J	H	0	0
	Zargasso	M	S/J	L	0	0
Capuchin monkeys	Cammello	M	A	H	0	0.3
	Cognac	M	A	H	0	0
	Paquita	F	A	M	0.5	0.5
	Pedro	M	S/J	H	1	1
	Pippi	F	A	L	0	0.5
	Quincey	F	S/J	M	0	0
	Roberta	F	A	M	0.5	0.8
	Robinhood	M	A	H	0.5	1
	Rubens	M	S/J	L	1	1
	Rucola	F	S/J	L	0	0
	Sandokan	M	S/J	H	1	1
	Vispo	M	S/J	H	0	0.5
Spider monkeys	1	F	S/J	L	0.5	0.8
	2	F	S/J	M	0	0
	3	M	S/J	H	0	0
	7	F	A	L	1	1
	9	F	A	L	0	0
	21	M	A	H	0	1
	24	F	S/J	L	1	1
	32	F	A	M	0	0
	34	M	A	M	0	0.3

Sex (F: female, M: male), age (A: adult, S/J: subadult or juvenile) and dominance rank (L: low, M: middle, H: high).

TABLE 3. For each test predictor included in the full model, estimates, standard errors (SE), confidence intervals (CIs), likelihood ratio tests (LRT), degrees of freedom (df), and *p* values (marked with an asterisk when significant), with reference categories in parentheses.

Predictors	Estimate	SE	2.5% to 97.5% CIs	*LRT*	*df*	*P*
Intercept	-2.37	1.87	-6.04 to 1.30	-	-	-
Novelty	1.16	0.45	0.27 to 2.05	7.16	1	0.007*
Species (gorillas)	5.20	2.43	0.44 to 9.97			
Species (macaques)	-4.87	1.95	-8.70 to -1.04			
Species (bonobos)	6.87	2.56	1.85 to 11.89	38.13	6	<0.001*
Species (chimpanzees)	0.42	1.89	-3.28 to 4.13			
Species (orangutans)	6.24	2.59	1.17 to 11.31			
Species (capuchin monkeys)	1.19	1.70	-2.14 to 4.52			
Age (subadults/juveniles)	-0.84	1.45	-3.67 to 2.00	0.34	1	0.559
Sex (males)	0.99	1.32	-1.60 to 3.58	0.56	1	0.454
Rank (low-ranking)	0.95	1.61	-2.20 to 4.11	0.70	2	0.704
Rank (middle-ranking)	-0.35	1.50	-3.29 to 2.58			

FIGURE 1. For each study species (i.e., Ch: chimpanzees, Bo: bonobos, Go: gorillas, Or: Sumatran orangutans, Ma: long-tailed macaques, Ca: tufted capuchin monkeys, Sp: spider monkeys), mean probability of interacting with objects. Circles and asterisks represent average values for each study subject. The thick horizontal lines represent the estimates of the model, which were back-transformed from the logit scale. The horizontal ends of the boxes represent the estimated standard errors, and the ends of the whiskers represent the 95% confidence intervals.