

# Curiosity in wild orangutans: ecological, social, and intrinsic effects assessed during a field experiment

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## Article

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# Abstract

The readiness to interact with, and explore, novel stimuli – i.e., curiosity – are cornerstones of innovation. Great apes show the broadest and most complex innovation repertoires. However, little is known about the factors that affect curiosity in wild apes. To shed light on wild apes' curiosity, we measured the reactions of wild Sumatran orangutans (*Pongo abelii*) to an experimental apparatus. Compared to adults, immatures showed higher tendencies to visually explore and approach the apparatus but were more likely to show signs of agitation. The presence of conspecifics who approached the apparatus increased exploration and approach tendencies. Prevailing habitat food availability positively affected exploration but had a negative effect on approach tendencies. These findings show that intrinsic, social, and ecological factors affect reactions to novelty in wild orangutans and suggest that exploration, neophobia and neophilia are independently regulated. Therefore, to understand the evolution of innovative tendency, factors acting on different elements of curiosity must be considered.

## Introduction

Although novel objects are rare in natural undisturbed habitats, where they do occur, they may afford important learning opportunities. As such, encountering and reacting to novel objects is one of the main pathways leading to innovations [1–6]. Individuals' reactions to novel objects are not just a reflection of their behavioral disposition [7] but also show how well they implement learning opportunities and how likely they are to make new innovations [8–12]. Individuals who are more prone to interact with and explore novel stimuli, and thus are more likely to engage with learning opportunities, develop adaptive skills and knowledge at a higher rate than more reluctant individuals. Skills and knowledge gained through innovation may increase an individual's survival and/or reproduction by enabling the exploitation of a novel resource or the use of a current resource more efficiently [9, 13, 14]. Therefore, how well individuals realize learning opportunities ultimately affects their fitness.

Reacting to novel stimuli includes two major elements: the readiness to interact with the stimuli (determined by the interplay of one's neotic responses) and the means which are used to investigate the stimuli (exploration). Neotic responses include neophilia, i.e. the spontaneous attraction to a novel stimuli, and neophobia, i.e. the spontaneous aversion towards it [4, 15]. Exploration describes the intensity and diversity of actions used to gather information about a stimulus through manipulation, visual examination, or any other kind of investigation [4, 16, 17]. Multiple lines of evidence from a range of taxa suggest that neophobia, neophilia and exploration are different mechanisms which are independently regulated and selected for [4, 16, 18–22].

The interplay of neotic responses and exploration is commonly used to study curiosity in animals, i.e., the motivation to know, learn and understand what is so far unknown [23, 24]. Whereas high levels of curiosity likely enhance the acquisition of fitness-relevant knowledge and skills, they also come with costs. Exploration is time intensive and potentially dangerous, just as high levels of neophilia bear a high risk of injury, poisoning, or predation [1, 4, 13, 25, 26]. These costs may outweigh the benefits of curiosity

in most conditions and life stages. Identifying the conditions which minimize these costs, will increase our understanding of how intrinsic curiosity can evolve. Ultimately, this may shed light on how selection can act on cognitive potential, and thus on the evolution of cognition and innovation ability.

Investigating curiosity in non-human great apes (henceforth great apes) can lend particular insight to our understanding of the evolution of complex cognition, including human cognition, as they are humans' closest relatives and have demonstrated high cognitive performance across different domains [e.g., 27, 28–30]. Furthermore, great apes show broad and complex innovation repertoires in the subsistence and comfort domains [31–33]. Several studies have looked at neotic responses and exploration in captive apes, but most focus on comparisons between species [7, 34, 35], whereas studies investigating factors that affect within-species variation in curiosity are relatively rare. In chimpanzees and orangutans, social interactions and social cues lead to lower levels of neophobia and increased exploratory tendencies [35–37]. Whereas in orangutans, human contact and social housing have a positive effect on individuals' exploratory tendencies [8, 38], in chimpanzees human demonstrators have no effect on neotic responses [39]. In chimpanzees, exploratory tendency decreases with increasing age [40].

Even less is known about great apes neotic responses and exploration in socially and ecologically relevant contexts, i.e., in the wild. Studies that have compared wild and captive great apes' responses to novelty revealed striking differences between the two settings [26, 41], suggesting that captive studies may have limited validity when it comes to understanding the underlying processes on the evolutionary level. Kalan and colleagues [42] assessed novelty reactions of wild African great apes and found that chimpanzees showed stronger looking impulses towards camera traps (novel stimuli) compared to bonobos and gorillas. Furthermore, among these three species, immature individuals, compared to adults, and solitary individuals, compared to those with association partners, spent more time looking at the camera traps [42], which is in line with the finding that juvenile chimpanzees are most likely to explore novel food items [43]. In terms of environmental factors, evidence from experiments with wild chimpanzees suggests that individuals are more likely to explore a novel foraging problem when they have a low, rather than high, energy balance [44]. Observational studies of wild great apes' natural, every-day exploratory behavior show that immatures have the highest exploration rates [45, 46]. Furthermore, in wild orangutans' exploration is socially induced on the developmental and proximate-immediate levels [47, 48], and more sociable populations tend to show higher exploration rates and larger innovation repertoires [47, 49].

These previous studies suggest that species, age, energy balance and social contexts can all influence great apes' curiosity in the wild. However, to fully comprehend the effects of these factors on neotic responses and exploratory tendencies, comprehensive testing of wild individuals is needed. Here, we aim to experimentally test which intrinsic and extrinsic factors affect curiosity in wild orangutans. Orangutans are especially suitable for this question because of their semi-solitary lifestyle and slow development, which allows for testing individuals of different ages in different social settings. We developed a novel experimental apparatus, and deployed it in the wild, to test wild habituated orangutans' reactions to novelty, including neophobia, neophilia, and exploration. Based on past studies of curiosity in captive

apes, novelty reactions in wild African apes, and naturally occurring exploration behavior in wild orangutans, we predicted that:

- I. Immature orangutans show higher exploratory tendencies, higher levels of neophilia and lower levels of neophobia than adults.
- II. The presence of association partners that themselves approach the apparatus reduces levels of neophobia and increases levels of neophilia and exploratory tendencies.
- III. Low prevailing habitat food availability leads to increased exploratory tendencies, decreased neophobia and increased neophilia.

## Methods

### Data collection

We collected data at the Suaq Balimbing monitoring station in the Gunung Leuser National Park in South Aceh, Indonesia during two periods: from June 2013 until March 2014 and from February 2019 until March 2020. If an individual participated in testing during both study periods, only trials from their first test period were included in our analysis, as that is when we can assume that the test apparatus was completely novel to them and avoids potentially confounding effects of a multi-year time gap between trials.

We conducted a total of 170 first period trials on 23 focal individuals, including 10 immatures (aged from 3 to 14 years), 6 mothers, and 8 unflanged males (i.e., adult males without secondary sexual characteristics). All focal individuals were already habituated to human observes, as part of long-term orangutan observation at the study site. Each individual participated in 1–27 trials (mean = 7.4 trials per individual). We excluded the data on immatures that were present during test trials but below the age of three years from the analysis, because they do not have the locomotor independence to approach the experimental apparatus on their own and are thus limited in how they can react to it. Furthermore, to ensure that we captured true novelty responses, the data on immatures that were present during the 2013–2014 study period and excluded because of their age, were also excluded from the 2019–2020 study period, even though they had by then reached the required age ( $N = 1$ ).

The trials took place during full day focal animal follows. The experimental apparatus (Fig. 1) was installed 5–20 meters away from the focal animal while the focal animal was resting or feeding in a relaxed state. Each trial began when the apparatus was installed in the canopy and ended when the focal individual retreated to more than 30 meters (after which we never saw a subsequent approach). Because we find and follow the orangutans opportunistically, we could not conduct the experiments after a predefined timeline. However, to control for their potential confounding effects, we include the number of previous trials and the exposure distance as random effects in our statistical models (see below).

The experimental apparatus was a *ca.* 65cm-long wooden log with a natural tree hole, which we filled with locally harvested forest honey. We additionally attached honeycombs to the outside of the apparatus, to increase the focal individuals' interest in the apparatus. The apparatus was hung from a branch in the canopy using a green plastic rope. To install the apparatus, we shot a stone, attached to a fishing line that was attached to the green rope, up over a tree branch using a hand-held wooden slingshot; the fishing line, and then green rope, were then pulled over the branch until the apparatus was well up into the canopy (10–20 meters high).

Because the trials were conducted in the trees, visibility was sometimes restricted. We therefore had 3 separate observers collecting data during the trials whenever possible: One observer filmed the focal animal, a second observer watched and narrated what they saw (which was recorded on the same or an additional camera that was used by the first observer, depending on the distance between the filming and narrating observer), and a third observer noted all measured parameters on a data sheet. All measured parameters were later obtained directly from the video, and missing elements were filled-in using the narration and/or, when needed, the data sheet.

## Variables

To quantify individuals' reactions to the apparatus, we measured 4 parameters, which served as response variables in our statistical models: A) looking duration (i.e., the number of seconds a focal was looking at the experimental apparatus during a trial) as a measure of exploration; B) approach latency (i.e., the time between when the experimental apparatus was in place and when the focal individual started to approach it) and C) approach distance (i.e., the distance over which the focal individual moved to approach the experimental apparatus which was calculated by subtracting the closest distance from the initial exposure distance), as measures of neophilia; and, D) behavioral indication of agitation (including scratching [50, 51], "kiss squeak," "grumble" and "grunt" vocalizations [52]) as a measure of neophobia.

To investigate what factors affected individuals' reactions to the apparatus, we used 1) the focal individuals' age-sex class, 2) the presence of an approaching party member (i.e., at least one association partner who decreased its distance to the apparatus during the trial, including all age sex classes of party members), and 3) the current habitat food availability. Food availability was quantified monthly via the number of trees bearing fruit in an established phenology plot in the study area which consisted of approximately 1000 marked trees (see [53] for details on the food availability data collection method). We included these three factors as predictor variables in our statistical models (see below).

To control for possible confounding external effects that could not be held constant, we included the initial exposure distance (i.e., the distance between the focal individual and the experimental apparatus when it was set up), and the exposure sequence (i.e., the number of trials the focal had participated in before the current trial) as fixed control effects.

## Statistical analyses

We analyzed and visualized the data using the R programming language [54], and RStudio [55]. To investigate the effects of the independent variables on the four dependent variables, we used linear mixed effect regression models (LMER) with a Gaussian family distribution (for the models with continuous response variables, i.e., looking duration, approach latencies, and approach distances) and a generalized linear mixed model (GLMM) with a Binomial family distribution (for the model with a binary response variable, i.e. the presence of signs of agitation), as implemented in the lme4 package [56]. Upon visual inspection of the distribution of each continuous response variable, we log transformed all three; looking duration ( $\log(\text{looking duration} + 1)$ ), approach latency ( $\log(\text{approach latency} + 1)$ ), and distance approach distance ( $\log(\text{distance change} + 1)$ ). We explored the most suitable random effect structure for our models using model selection via likelihood ratio tests with the *anova* function [57, 58]. Model selection indicated that we should use models with no random intercepts or random slopes. However, most focal individuals contributed to multiple data points (i.e., participated in multiple trials, see above) and thus, to avoid pseudo replication issues, we included the focal individual as a random intercept in all our statistical models. Following this procedure, all models converged, and none had singularity issues.

For each of the four models, we first tested the overall fit of the model by comparing the full model (including all predictor variables and random effect) with the null model (including only random effect and control variables) using a likelihood ratio test with the *anova* function [57, 58]. All full models were supported (see results), and so we assessed the significance of the predictor variables via their p-values in the full model (in the case of the GLMM with a Gaussian family distribution, the p-values were computed with the *cf-test* function from the multcomp package [59]). We investigated differences between the age-sex classes using posthoc tests as implemented in the *glht* function of the multcomp package [59].

We visually examined all model fits to assess whether they satisfied model assumptions (for the LMERS this included normally distributed model residuals, homogeneity of the variance, and normally distributed random effects) and to check for the presence of influential observations [60]. For the Binomial GLMMs, we tested for overdispersion and zero inflation as implemented in the DHARMA package [61]. We checked all models for multicollinearity with the *check\_collinearity* function of the performance package [65]. We did not find any evidence for multicollinearity issues in our models (variance inflation factors ranged from 1.02 to 1.24 across the models and factors).

To assess the overall goodness-of-fit of the models, we used model  $R^2$  values, which we retrieved via the r2glmm package [62] following [63]. We assessed the stability of all our mixed models on the level of the random effects by dropping levels one-by-one. We found that the direction of the effects of the predictor variables on the response variables were consistent across model recomputations.

For the plots, we used the ggplot2 and cowplot packages [64, 65], and calculated the marginal effects of each predictor variable (while holding all other variables at their means) from each corresponding model using the *ggeffects* function of the ggeffects package [66]. For plots based on models with log transformed response variables, we back transformed the predictions so that the y-axes are on the original scale of the measured variable rather than on the log scale.

## Ethics statement

All our research protocols were approved by the Ministry of Research, Technology and Higher Education (RISTEKDIKTI; Research Permit No.: 54/E5/E5.4/SIP/ 2019 and following) and adhered to the legal requirements of Indonesia.

## Results

### General model fits

Model comparison showed that the four full models fitted the data better than their respective null models, indicating an overall effect of the predictor variables on the response variables (LRTs full model versus null model: looking duration (model A): Chi-square = 27.68,  $P < 0.001$ ; approach latency (model B): Chi-square = 19.352,  $P < 0.001$ , distance change (model C): Chi-square = 51.54,  $P < 0.001$ ; agitation (model D): Chi-square = 9.08,  $P = 0.055$ ).

### Differences between age-sex classes in reactions to experiment apparatus

We found that immature individuals looked significantly longer at the experimental apparatus than mothers and than unflanged males, and that mothers looked significantly longer at the apparatus than unflanged males (Table 1 – model A, Fig. 2A). Immature individuals had significantly shorter latencies to approach the experimental apparatus than mothers and unflanged males but there was no significant difference in approach latencies between mothers and unflanged males (Table 1 – model B, Fig. 2B). There was a trend for immatures to approach closer to the experimental apparatus (measured by distance change towards the apparatus and controlled for initial exposure distance) than mothers but no evidence for differences in approach distances between the other age-sex classes (Table 1 – model C, Fig. 2C). Immatures also had a higher probability of showing signs of agitation during the experimental trials compared to unflanged males, while there were no differences in agitation probability between the other age-sex classes (Table 1 – model D, Fig. 2D).

### Effects of association partners on reactions to the experiment apparatus

Association partners who approached the apparatus had a significant positive effect on focal individuals' looking durations at the experimental apparatus (Table 1 – model A, Fig. 3A) but no effect on their latencies to approach the apparatus (Table 1 – model B, Fig. 3B). Furthermore, individuals approached significantly closer to the experimental apparatus (measured by distance change towards the apparatus controlled for the initial exposure distance) when there was a party member present who also approached the apparatus (Table 1 – model C, Fig. 3C). The probability that the focal individual showed signs of

agitation was not affected by the presence of party members who approached the apparatus (Table 1 – model D, Fig. 3D).

## **Effects of food availability on reactions to the experiment apparatus**

Habitat food availability had a significant positive effect on looking durations at the experimental apparatus (Table 1 – model A, Fig. 4A) and a trend for a positive effect on latencies to approach the experimental apparatus (Table 1 – model B, Fig. 4B). Habitat food availability had no effect on how closely individuals approached the experimental apparatus (measured by distance change towards the apparatus controlled for initial exposure distance, Table 1 – model C, Fig. 4C), and no effect on the probability that the focal individual would show signs of agitation during the experimental trial (Table 1 – model D, Fig. 4D).



Table 1

**Intrinsic, environmental, and social effects on reactions to the experiment apparatus.** Effects of age sex class of the focal individual, food availability, the presence of party members who approached the apparatus on A) looking duration, B) approach latency, C) approach distance and D) agitation probability (i.e., the presence of signs of agitation), controlled for the initial exposure distance, trial sequence (i.e., the number of previous trials). Including estimate, standard errors, p-values and  $R^2$  values, analysed with GLMMs with a Gaussian or Binomial family distribution. Looking durations, approach latencies and distance changes were log transformed ( $\log(x + 1)$ ). Significant p-values at the 5% level are bolded and trends at the 8% level are underlined.

| Model | Response         | Factors                 | Factor Type | Estimate | Std. Error | P-Value        | $R^2$ | Distribution |
|-------|------------------|-------------------------|-------------|----------|------------|----------------|-------|--------------|
| A     | Looking duration | Intercept               | Intercept   | 3.865    | 0.789      | < 0.001        | 0.38  | Gaussian     |
|       |                  | Age Sex Class           | Predictor   |          |            |                |       |              |
|       |                  | Immatures - Mothers     |             | -1.448   | 0.593      | <b>0.029</b>   |       |              |
|       |                  | Immatures - Unfl. Males |             | -2.902   | 0.597      | < <b>0.001</b> |       |              |
|       |                  | Mothers - Unfl. Males   |             | -1.454   | 0.676      | <b>0.031</b>   |       |              |
|       |                  | Food availability       | Predictor   | 0.182    | 0.067      | <b>0.007</b>   |       |              |
|       |                  | Party approached        | Predictor   | 0.671    | 0.291      | <b>0.021</b>   |       |              |
|       |                  | Exposure distance       | Control     | -0.062   | 0.026      | 0.019          |       |              |
|       |                  | Trial sequence          | Control     | -0.017   | 0.025      | 0.494          |       |              |
|       |                  | Individual              | Random      |          |            |                |       |              |
| B     | Approac Latency  | Intercept               | Intercept   | -0.792   | 0.550      | 0.150          | 0.28  | Gaussian     |
|       |                  | Age Sex Class           | Predictor   |          |            |                |       |              |
|       |                  | Immatures - Mothers     |             | 0.653    | 0.290      | <b>0.048</b>   |       |              |
|       |                  | Immatures - Unfl. Males |             | 1.263    | 0.330      | < <b>0.001</b> |       |              |
|       |                  | Mothers - Unfl. Males   |             | 0.610    | 0.373      | 0.102          |       |              |
|       |                  | Food availability       | Predictor   | 0.099    | 0.051      | 0.054          |       |              |

| Model | Response          | Factors                 | Factor Type | Estimate | Std. Error | P-Value        | R <sup>2</sup> | Distribution |
|-------|-------------------|-------------------------|-------------|----------|------------|----------------|----------------|--------------|
|       |                   | Party approached        | Predictor   | -0.006   | 0.250      | 0.980          |                |              |
|       |                   | Exposure distance       | Control     | 0.035    | 0.019      | 0.065          |                |              |
|       |                   | Trial sequence          | Control     | 0.047    | 0.017      | 0.007          |                |              |
|       |                   | Individual              | Random      |          |            |                |                |              |
| C     | Approach distance | Intercept               | Intercept   | 0.190    | 0.378      | 0.615          | 0.39           | Gaussian     |
|       |                   | Age Sex Class           | Predictor   |          |            |                |                |              |
|       |                   | Immatures - Mothers     |             | -0.577   | 0.249      | 0.062          |                |              |
|       |                   | Immatures - Unfl. Males |             | -0.256   | 0.266      | 0.554          |                |              |
|       |                   | Mothers - Unfl. Males   |             | 0.321    | 0.295      | 0.554          |                |              |
|       |                   | Food availability       | Predictor   | 0.016    | 0.033      | 0.632          |                |              |
|       |                   | Party approached        | Predictor   | 1.085    | 0.138      | < <b>0.001</b> |                |              |
|       |                   | Exposure distance       | Control     | 0.043    | 0.013      | < 0.001        |                |              |
|       |                   | Trial sequence          | Control     | 0.008    | 0.012      | 0.511          |                |              |
|       |                   | Individual              | Random      |          |            |                |                |              |
| D     | Agitation         | Intercept               | Intercept   | 2.068    | 1.181      | 0.080          | 0.13           | Binomial     |
|       |                   | Age Sex Class           | Predictor   |          |            |                |                |              |
|       |                   | Immatures - Mothers     |             | -0.840   | 0.619      | 0.321          |                |              |
|       |                   | Immatures - Unfl. Males |             | -2.189   | 0.895      | <b>0.043</b>   |                |              |
|       |                   | Mothers - Unfl. Males   |             | -1.349   | 0.962      | 0.321          |                |              |
|       |                   | Food availability       | Predictor   | -0.121   | 0.105      | 0.249          |                |              |

| Model | Response | Factors           | Factor Type | Estimate | Std. Error | P-Value | R <sup>2</sup> | Distribution |
|-------|----------|-------------------|-------------|----------|------------|---------|----------------|--------------|
|       |          | Party approached  | Predictor   | 0.218    | 0.438      | 0.618   |                |              |
|       |          | Exposure distance | Control     | -0.083   | 0.048      | 0.083   |                |              |
|       |          | Trial sequence    | Control     | -0.114   | 0.043      | 0.008   |                |              |
|       |          | Individual        | Random      |          |            |         |                |              |

## Discussion

The aim of this study was to investigate how intrinsic and extrinsic factors affect curiosity, i.e., neotic responses and exploratory tendencies in wild orangutans. Our results showed that age, the presence of association partners that approached the apparatus, and food availability significantly affected levels of neophobia, neophilia, and exploration shown towards a novel experimental apparatus.

We found that immatures spent significantly more time visually exploring the experimental apparatus than adults (Fig. 1A, Table 1) and showed higher levels of neophilia (i.e., significantly shorter approach latencies and a trend for approaches to closer distances) than adults. This is in line with findings on exploratory tendency and neophilia from a variety of species tested in captivity including primates, bats, dogs, hyaenas, and several bird species [9, 16, 40, 67–74]; But see [22, 34, 75]). Furthermore, in wild African great apes, immatures show stronger looking reactions to novel camera trap devices [42] and are more likely to explore novel food items than other age classes [43]. On the proximate immediate level, higher exploratory tendencies and neophilia in immatures can be explained by the Spare-time Hypothesis, which states that youngsters have more free time available because they experience reduced environmental stress (such as the need to find food or to be vigilant, which are usually taken care of by their caregivers and/or other group members) and social distractions (such as the ones resulting from mating and reproduction) [22, 25]. However, in our study, 5 of the 8 immature focal individuals were independently ranging juveniles. These independent juveniles need to sustain their growing bodies, while they range largely on their own or in small playful peer groups, and thus likely experience increased environmental stress and social distractions. From an evolutionary perspective, it stands to reason that immatures have an innate disposition to be exploratory and neophilic because they need to learn about their environment to develop their skill and knowledge repertoires [Needing to Learn Hypothesis: 76]. For young individuals, the whole world is novel, and thus having temporary mechanisms in place which ensure that they can learn about the world is certainly adaptive [77]. Higher exploratory and neophilic tendencies in immatures enable learning about resources and thus to sustain themselves are also in line with the Necessity Hypothesis, which sees ecological needs as the biggest drivers of innovation (see below) [1, 4, 73, 78].

Interestingly and against our initial prediction, our findings showed that wild immature orangutans have a stronger neophobic reaction to the experimental apparatus than adults, in that they were more likely to show signs of agitation during the experimental trials. If high levels of exploration and neophilia in immatures ensure that learning opportunities are realized, high levels of neophobia may serve to protect them from potential dangers while doing so [4, 26, 34]. A certain level of agitation/excitement and alertness when exploring novel stimuli may ensure that risks of predation and injury are minimized, while the heightened/excitement-induced awareness may also improve memory retention and ultimately increase connection formation and therefore learning [reviewed by 79]. According to the Dangerous Niche Hypothesis, species and individuals which are exposed to higher risks should show higher levels of neophobia [4]. The combination of a small body size and semi-solitary lifestyle indeed likely puts immature orangutans at increased ecological risk. However, from our results, it remains unclear if immature orangutans have an intrinsic tendency to be more neophobic than adults or if their neophobic reactions were triggered by them confronting the stimulus more closely (see above). High levels of neophobia in combination with high levels of neophilia and exploration have been suggested to be a great ape characteristic [26] and have also been found in several bird species, including corvids and psittacines which are among the most innovative bird taxa [4, 19, 80].

In terms of the effects of social factors, we found that visual exploration, and to some extent neophilia (measured in approach distances), increased when at least one association partner was present that approached the experimental apparatus (Figs. 2A and C, Table 1). Consistent with these results, wild orangutans' natural exploration behavior is positively affected by associations on the developmental and immediate proximate level [47, 48]. Increased levels of neophilia through social effects are in line with a large number of findings across a variety of taxa [reviewed by 26]. However, somewhat in contrast to our findings, African great apes show shorter visual exploration of novel stimuli with increasing number of current association partners [42]. Interestingly, this study of African apes did not take the behavior of the association partners into account. Therefore, the seemingly contrasting results may imply that response-specific facilitation leads to increased exploration of a novel stimuli but not general social facilitation. The Social Information Hypothesis states that individuals confronted with novel stimuli should rely on social cues to assess if the stimuli is worth it and safe to explore [26, 41]. Forss et al. [26] explain the innovation paradox, i.e., that large innovation repertoires are often found in slowly developing species that show a combination of high levels of neophobia and high exploratory tendency: high levels of intrinsic neophobia can be overcome by social information obtained from experts. Our results suggest that rather than affecting neophobia per se, response facilitation leads to an increased likelihood that individuals investigate novel stimuli and increases the intensity with which they explore the stimuli.

As to environmental effects, we found that high food availability (and thus, likely, high energy levels) correlates with increased visual exploration of the experimental apparatus. However, we also found a trend for lower levels of neophilia (shown in longer latencies to approach the experimental apparatus) when food availability was high. In the innovation literature, there is an ongoing debate about whether necessity or opportunity is the mother of invention, i.e., whether individuals are more prone to innovate when they experience the ecological pressure to do so (e.g., during food shortages or periods of increased

energetic stress), or when they encounter suitable ecological conditions and stimuli (e.g., the resources and materials needed for innovations) and/or have increased amounts of energy and time available [44, 78, 81, 82]. In line with the Opportunity Hypothesis, our results suggest that high energy levels lead to an increased investment in gaining information about a novel stimulus. However, the trend towards a negative effect of food availability on neophilia may mean that it is during low energy periods when the stimulus is indeed actively investigated. If an individual's energetic state affects exploration and neophilia in different directions, novel stimuli are most likely turned into innovation at a certain optimal level of prevailing ecological pressure, rather than at its extremes. Notably, however, for the Suaq Balimbing population, habitat food availability is generally higher than for most other orangutan populations. The experienced food availability over the course of this study ranged from 5.8 to 14.0. For most orangutan populations, the lower part of this range is around or above the yearly maximum. Therefore, with our experiment, we are likely unable to properly assess the effects of low food availability on wild orangutans' curiosity.

Our findings may have important implications for experimental behavioral testing of animals, including cognitive tests where it can be difficult to differentiate between low level performance and a lack of motivation to interact with an experimental apparatus. This is particularly true in the wild, where long habituation periods are often not possible. When testing individuals, the first step is to get them to participate in the experiment. This includes overcoming their fear of the testing procedure and ensuring their motivation to interact with it [26]. Our results imply that individuals' readiness to participate in behavioral experiments is likely affected by their age, as well as social and environmental factors. These factors should thus all be taken into account when conducting behavioral experiments in the wild.

## **Conclusion**

Our results suggest that immature wild orangutans are more exploratory and neophilic than adults but also more neophobic, a combination which likely allows them to learn safely about their environment. Furthermore, response facilitation through conspecifics increases exploration and neophilia in wild orangutans, despite their semi-solitary lifestyle. High energy levels lead to an increased investment in gaining information about a novel stimulus, but it may be during low energy periods when the stimulus is indeed actively investigated. Overall, the age effects had larger effect sizes on than the effects of association partners or food availability. In other words, wild orangutans are most likely to realize learning opportunities presented by novel stimuli when they are young while the presence of association partners that show a positive reaction to the stimuli, and favorable ecological conditions may further increase their readiness to do so. Therefore, over evolutionary time, extended periods of immaturity, opportunities to depend on the knowledge of conspecifics, and favorable ecological conditions are likely to bring about high levels of innovativeness.

## **Declarations**

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### **Author contributions**

CS co-conceptualized and designed the study, conducted experimental trials, analysed the data, and wrote the manuscript. LN conducted experimental trials, organized, and processed the data and provided feedback on the manuscript. LAC conducted experimental trials, helped processing the data and provided feedback on the manuscript. AMA visualized the data, edited the manuscript text, and provided feedback on the manuscript. NOC conducted experimental trials and provided feedback on the manuscript. TR and IL provided feedback on the manuscript. DH co-conceptualized the study and provided feedback on the manuscript.

### **Conflicting interests**

The authors declare that they have no conflicting interests.

### **Data availability**

All data analyzed during this study are included in the supplementary information files of this article (table A1).

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## Figures

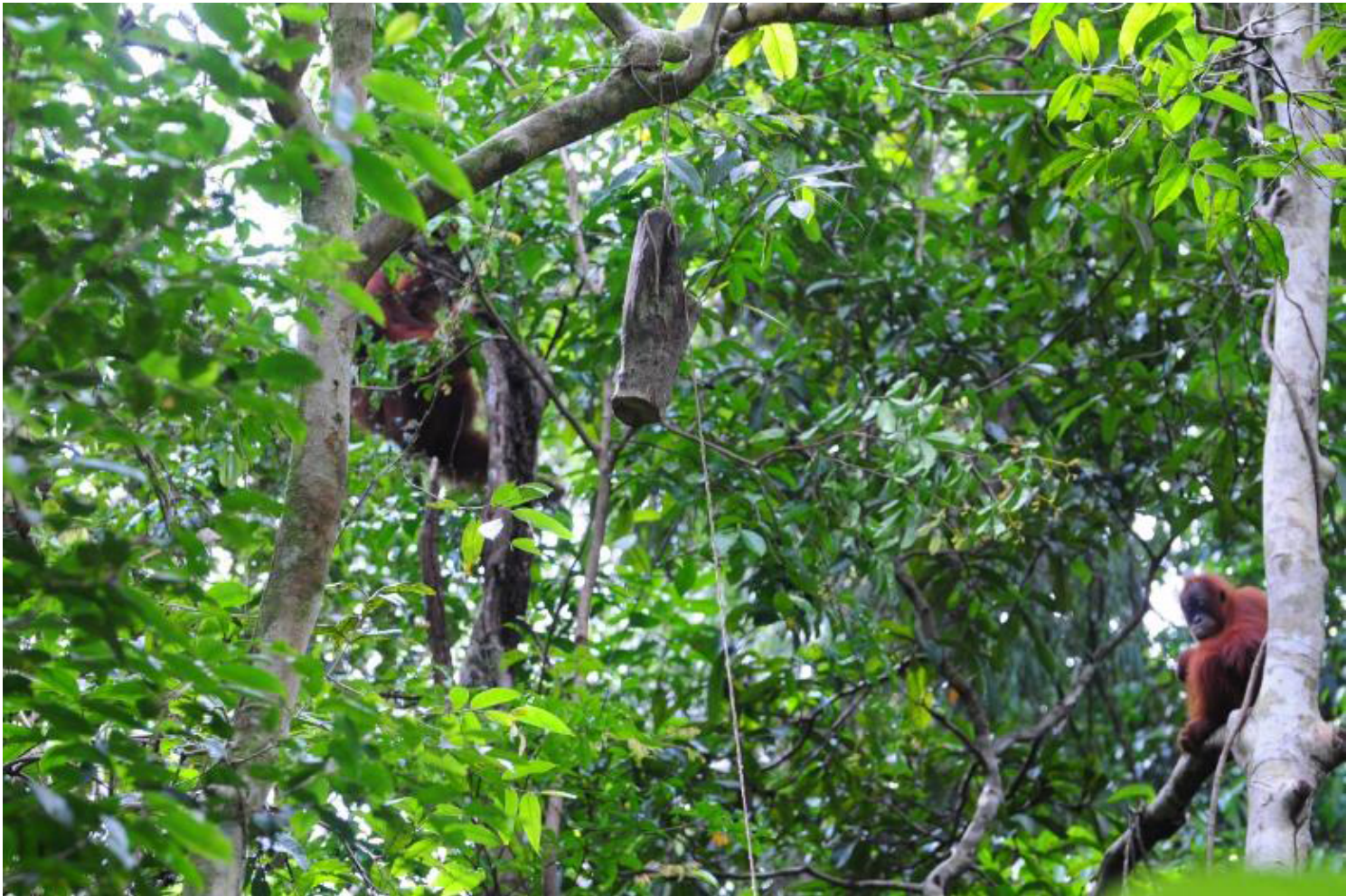
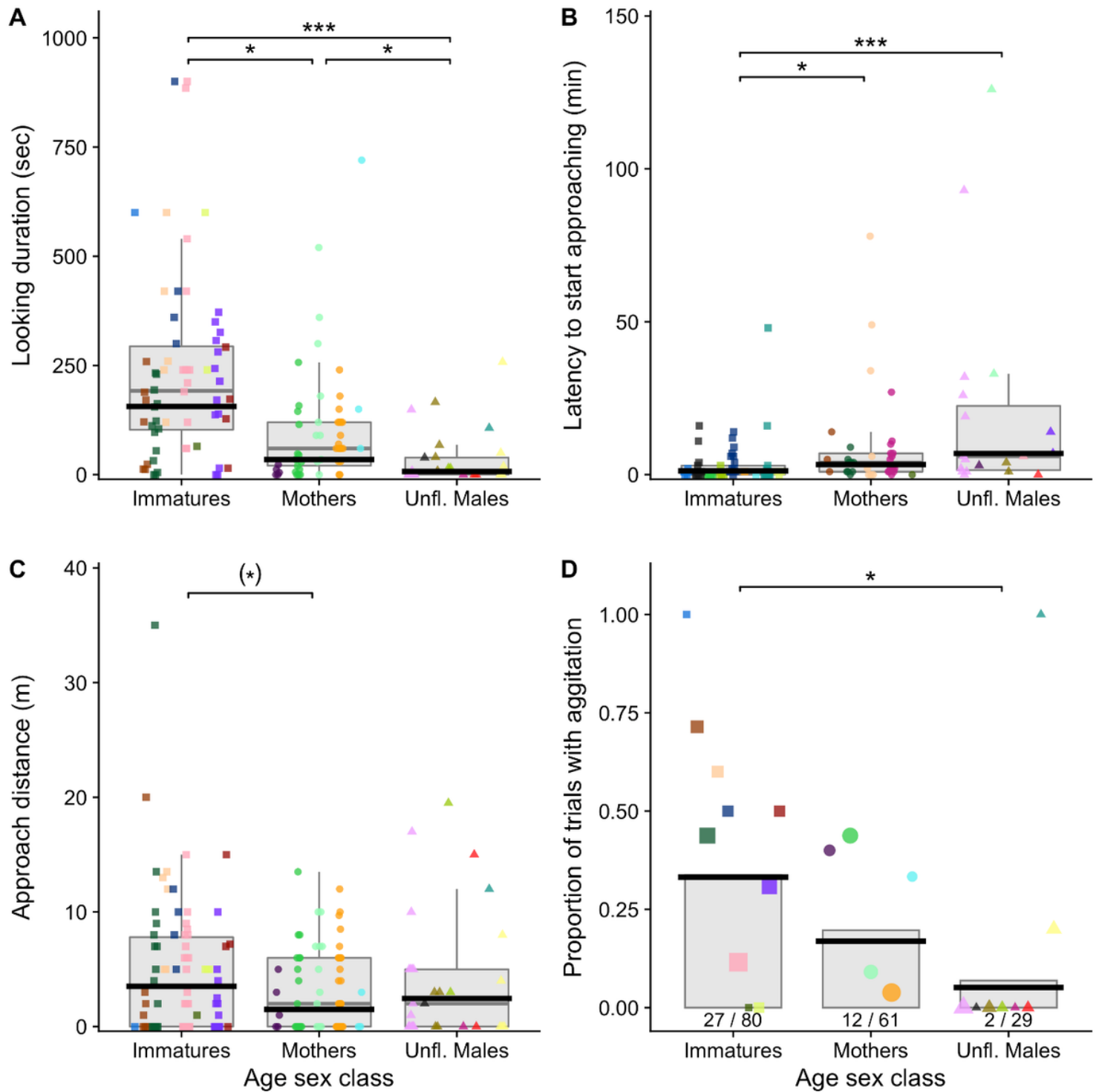


Figure 1

**Experimental apparatus and set up.** Experimental trial with the set-up experiment apparatus and two focal orangutans in the background.



**Figure 2**

**Differences between age sex classes in reactions to the experiment apparatus.** A) Looking durations at the experimental apparatus, B) latencies to approach the experimental apparatus, C) approach distances towards the experimental apparatus, and D) the probability of signs of agitation during the experimental trial for immatures, mothers and unflanged males. For panels A – C, each data point represents one experimental trial on one focal individual with colors referring to different individuals. The grey boxes show the interquartile ranges, the whiskers extend to the maximum and minimum data points that are

within 1.5 times the interquartile range from the upper and lower quartiles, and the grey horizontal lines represent the medians. For panel D, the grey columns represent the average proportion of trials with agitation for each age-sex class (with the number of trials with agitation over the total number of trials per age-sex class indicated under each grey bar) and the data points each show one individual's proportion of trials with agitation; the size of each data point represents the number of trials for that individual. In all panels, the thick black horizontal lines represent mean model predictions when holding all other predictor variables at their means.

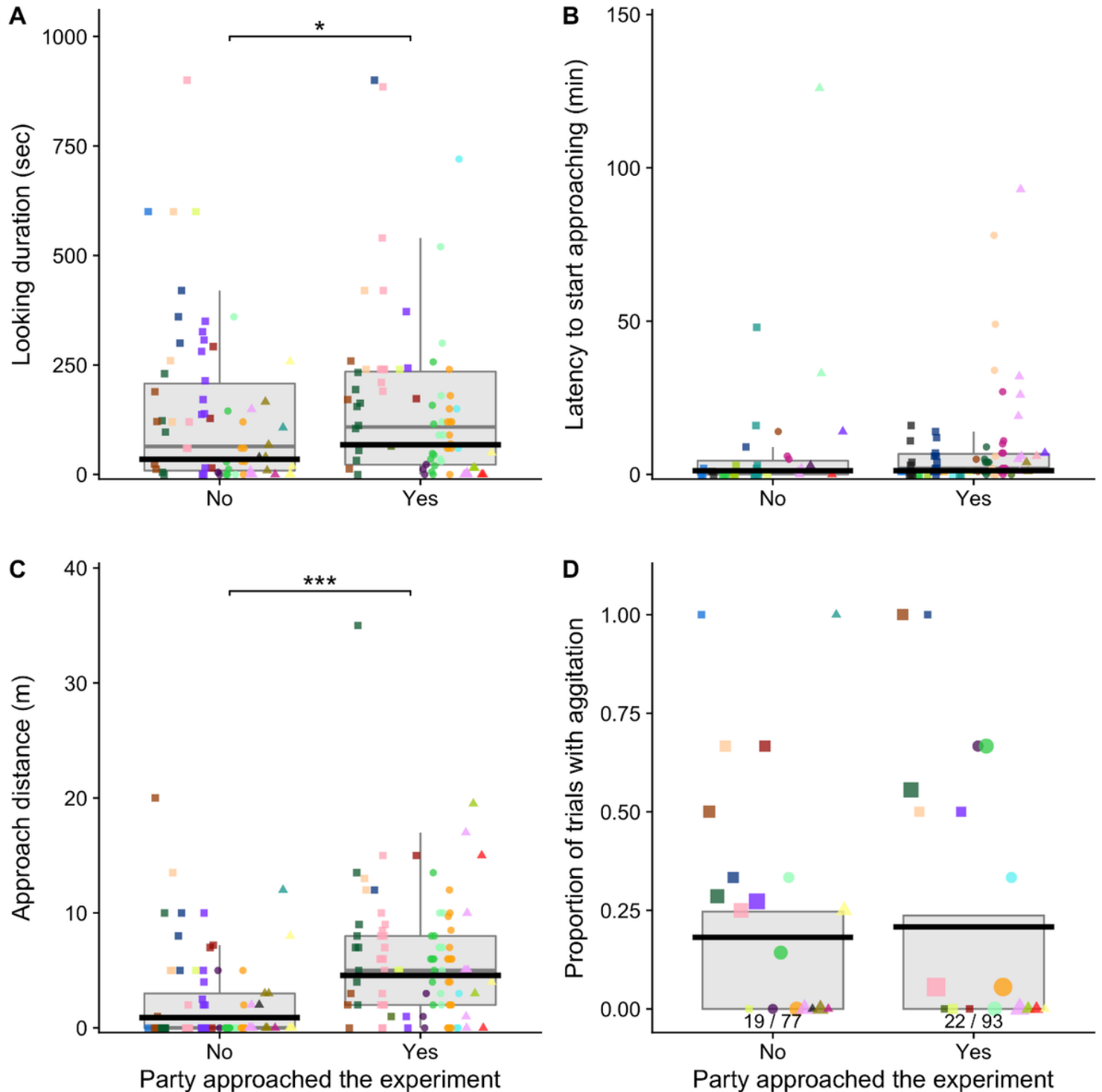
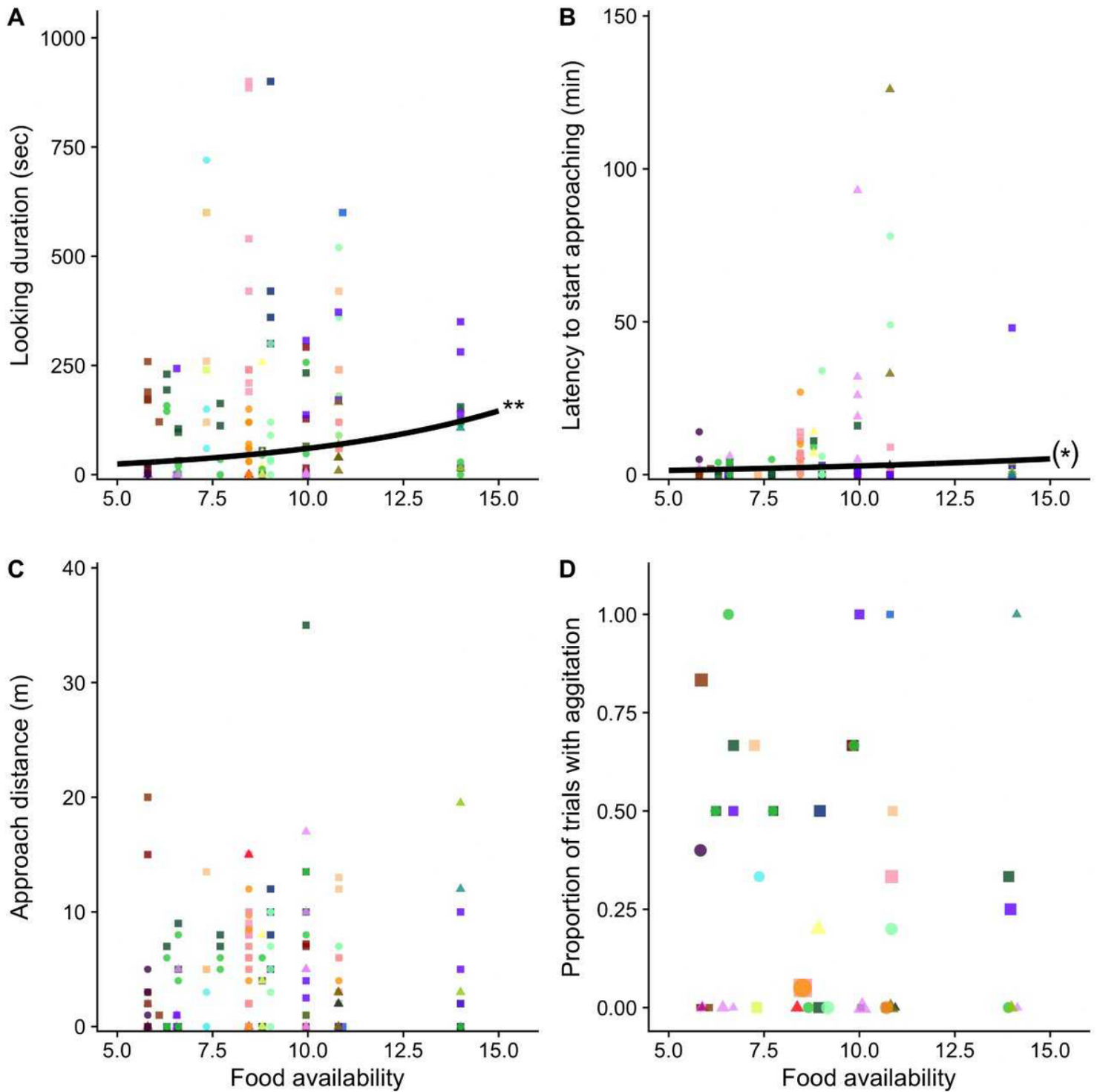


Figure 3



**Effects of association partners on reactions to the experiment apparatus.** A) Looking durations at the experimental apparatus, B) latencies to approach the experimental apparatus, C) approach distances towards the experimental apparatus, and D) the probability of signs of agitation during the experimental trial when there was no association partner (party) approaching the experimental apparatus versus when there was. For panels A – C, each data point represents one experimental trial on one focal individual with colors referring to different individuals. The grey boxes show the interquartile ranges, the whiskers extend to the maximum and minimum data points that are within 1.5 times the interquartile range from the upper and lower quartiles, and the grey horizontal lines represent the medians. For panel D, the grey columns represent the average proportion of trials with agitation for each age-sex class (with the number of trials with agitation over the total number of trials per age-sex class indicated under each grey bar) and the data points each show one individual's proportion of trials with agitation; the size of each data point represents the number of trials for that individual. In all panels, the thick black horizontal lines represent mean model predictions when holding all other predictor variables at their means.



**Figure 4**

**Effects of food availability on reactions to the experiment apparatus.** A) Looking durations at the experimental apparatus, B) latencies to approach the experimental apparatus, C) approach distances towards experimental apparatus and D) the probability of signs of agitation during the experimental trial as a function of habitat food availability. For panels A – C, each data point represents one experimental trial on one focal individual with colors referring to different individuals, and shape showing their age-sex class (square = immature, circle = mother, triangle = unflanged male). The thick black lines represent

mean model predictions across food availability values for significant effects, when holding all other predictor variables at their means. For panel D, the data points each show one individual's proportion of trials at that food availability value with agitation; the size of each data point represents the number of trials for that individual at that food availability value. Note that points in panel D have been slightly jittered horizontally, to ensure that all points are visible.

## Supplementary Files

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- [TableA1.xlsx](#)