

Neophobia across social contexts in juvenile herring gulls

Reinoud Allaert^{1,2}, Sophia Knoch^{2,3}, Simon Braem^{1,2}, Dries Debeer⁴, An Martel^{2,5}, Wendt Müller⁶, Eric Stienen⁷, Luc Lens^{1,2}, & Frederick Verbruggen^{1,2,3}

¹ Dept. Biology, Ghent University

² Centre for Research on Ecology, Cognition and Behaviour of Birds

³ Dept. Experimental Psychology, Ghent University

⁴ Research Support Office, Faculty of Psychology and Educational Sciences,

⁵ Dept. Pathobiology, Pharmacology and Zoological Medicine, Ghent University

⁶ Dept. Biology, Antwerp University

⁷ Research Institute for Nature and Forest

Correspondence: reinoud.allaert@ugent.be

Abstract

Neophobia, the fear or avoidance of the unfamiliar, can have significant fitness consequences. It is typically assessed by exposing individuals to unfamiliar objects when they are alone, but in social species the presence of conspecifics can influence neophobia. However, previous research on the effect of group dynamics on neophobic responses has produced mixed results. Here, we explore the degree of neophobia of an individual in different social contexts in a highly social species, the herring gull. We hypothesise that the distribution of neophobic responses will change in a group context. Specifically, we expect less variance between individuals when tested in a group than when tested individually. However, how much and in what direction the average neophobic response will change, will depend on the social mechanisms at play. To test these predictions, we will expose juvenile herring gulls to novel objects in both individual and group settings, and we will repeat each condition twice to establish replicability.

Keywords: Animal Behaviour, Behavioural Inhibition, Neophobia, Social Behaviour, Herring Gull, Animal Personality

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

Introduction

16

Neophobia is the fear or reluctance to engage with new or unfamiliar objects, places or scenarios. It is often considered to be a consistent personality trait across species, affecting an individual's survival and adaptation (Both et al., 2005; Greggor et al., 2015; Kimball and Lattin, 2023; Vrublevska et al., 2015). Research into animal behaviour is increasingly focusing on neophobia because of its significance in the context of rapid environmental change. The world is rapidly urbanising, with the footprint of urban land cover expected to at least double by the end of the century (Gao and O'Neill, 2020). Many species must therefore adapt to human-induced changes in their environment, and hence, to unfamiliar scenarios (Lee and Thornton, 2021; McKinney, 2002). In such situations, neophobia can, on the one hand, serve as a survival mechanism, allowing individuals to avoid potential threats and increase their chance of survival (Greenberg and Mettke-Hofmann, 2001). On the other hand, excessive aversion to novelty can restrict exploratory behaviour, limiting an individual's ability to locate and exploit novel resources, learn from its novel environment and adapt to environmental changes (Biondi et al., 2010; Greenberg, 2003).

To assess neophobia, individuals are typically exposed to novel food, objects, or spaces (Greggor et al., 2015; Mettke-Hofmann, 2017). For example, in the 'novel object task', which we use in the present study, an individual encounters an unfamiliar object, often placed next to a food reward, in a familiar environment. The latency to approach the food (in the presence of the novel object) or to interact with the novel object itself, is then used as a measure of neophobia (Greggor et al., 2015; Miller, Lambert, et al., 2022; Vernouillet and DM Kelly, 2020). These measures have been used in cross-species comparisons to investigate, for example, the socio-ecological drivers of neophobia (Mettke-Hofmann et al., 2002; Miller, Lambert, et al., 2022), or within species, to investigate both the causes and consequences of individual differences in neophobia (Greenberg and Mettke-Hofmann, 2001).

Most research on neophobia has focused on individual animals, both in laboratory and field settings. However, it is important to consider that many species are to various extents reliant on social information, so individuals can influence each other's behaviour. This is also true in the context of adapting to environmental changes and urbanisation (Lee and Thornton, 2021). For instance, when individuals encounter a new environment, they may learn from others about appropriate roosting or nesting sites, food sources, or unfamiliar predators (Harel et al., 2017; Keen et al., 2020; Loukola et al., 2012). In this context, several studies suggest that the presence of conspecifics also influences neophobia. However, the mechanisms behind this social phenomenon are still a topic of debate due to the various patterns that have been observed.

First, some studies have found that individuals in groups are generally less neophobic than when tested alone. For example, Coleman and Mellgren presented zebra finches (*Taeniopygia guttata*) with novel feeders and decorated the feeders with novel objects (Coleman and Mellgren, 1994). Individuals in a group approached and started using the new and decorated feeders more quickly than when tested alone. Other studies reported similar patterns in different species for some (but not necessarily all) measures of neophobia (Benson-Amram and Holekamp, 2012; Kareklas et al., 2018; Moretti et al., 2015; Soma and Hasegawa, 2004). Such mitigating effects of social context on neophobia may be attributed to 'risk dilution' (Krause and Ruxton, 2002) or 'social buffering' (Kikusui et al., 2006). These theories predict that neophobia, or fear responses in general, are reduced in the presence of others, as individuals in a group collectively share the potential risks associated with novel situations or threats, causing them to behave more similarly.

Second, some studies found the opposite pattern. For example, common ravens (*Corvus corax*) and carrion x hooded crows (hybrid; *C. corone*, *C. cornix*) approached novel objects faster when alone than when accompanied by a conspecific (Miller, Bugnyar, et al., 2015; Stöwe, Bugnyar, Heinrich, et al., 2006; Stöwe, Bugnyar, Loretto, et al., 2006). Other studies have observed similar patterns in other species, including Indian mynahs, *Acridotheres tristis* (Griffin et al., 2013), house sparrows, *Passer domesticus* (TR Kelly et al., 2020), and even zebra finches (Kerman et al., 2018; St. Lawrence et al., 2021), thus failing to replicate the findings of the aforementioned study by Coleman and Mellgren (1994). Interestingly, however, some of these studies found that once

individuals reached the novel object, they spent more time interacting with it when in the presence of others (either in pairs or in groups) than when isolated (Miller, Bugnyar, et al., 2015; St. Lawrence et al., 2021; Stöwe, Bugnyar, Heinrich, et al., 2006). It has therefore been suggested that the slower approach latencies may be due to conspecifics 'negotiating', by using behavioural cues to coordinate their actions and deciding who will approach the novel object first. Consequently, this may lead to a convergence of individual behaviours, as group members align their actions based on these cues.

Third, some studies failed to find effects of social context on average neophobic responses altogether (e.g Apfelbeck and Raess, 2008). While, it is of course possible that social context does not matter for some species, it is also possible that the presence of conspecifics alters behaviour of individuals without changing the mean response. Specifically, in environments where conspecifics' behaviour serves as an indicator of appropriate responses, individuals may adjust their own behaviour to match that of others (Herbert-Read et al., 2013). This synchronisation of behaviours within the group, or 'social conformity', enhances cohesion and helps the group to adapt to their environment. For example, observations in a variety of species, such as zebra finches (Schuett and Dall, 2009) and gouldian finches, *Erythrura gouldiae* (King et al., 2015), show how individuals adapt their behaviour and mirror their partners' character traits. For instance, if a gouldian finch exhibited bold behaviour, the observing individual tended to become bolder as well, while if the partner displayed shyness, the observing individual mirrored this trait. Thus, this study found that the neophobic response was similar on average for individuals tested alone or in pairs, but there was less variation between individuals in the paired condition compared to the alone condition.

Current study The aim of this study is to investigate if and how the social context affects neophobia in the herring gull (*Larus argentatus*). Gulls' natural coastal habitat is rapidly disappearing, forcing them to live closer to humans in urban environments and to rely more on anthropogenic food sources (Coulson, 2015; Nager and O'Hanlon, 2016). Although reports in popular media may suggest that herring gulls are generally not neophobic due to their approach towards humans or stealing food, such anecdotes do not necessarily reflect the species' behaviour at a population level (Inzani et al., 2023). In fact, significant levels of neophobia as well as individual differences therein exist within populations (Inzani et al., 2023). The latter finding suggests that for some individuals, it might be easier to adapt to environmental change and urbanisation than for others. Indeed there is considerable intraspecific variation in how herring gulls utilise urbanised areas, ranging from minimally to almost complete dependence (O'Hanlon et al., 2017; Pavlova and Wronski, 2020). Herring gulls are a highly social species, utilising cues not only from conspecifics, but even from other species, including humans. This suggests that social learning is a key aspect of gull behaviour (Feist et al., 2023; Frings et al., 1955; Gandolfi, 2009; Goumas et al., 2020). Thus, when assessing their neophobia, it is important to do this not only in an individual context, but also in a social (group) context.

Based on previous findings, we predict that the distribution of neophobic responses will depend on the social context. However, the direction of the effects will depend on the social mechanisms at play. In [Figure 1](#), we provide a template for testing the three different hypotheses of group effects, taking into account two measures, namely the average neophobic response and the variance between individuals.

Overall, we predict that there will be lower variance between individuals when they are tested in a group, compared to when they are tested alone. After all, all of the major hypotheses discussed above assume that individuals become more similar to each other by spreading risk, jointly buffering stress, negotiating with each other, or simply through social conformity. However, there are three possible scenarios regarding the average neophobic response. First, the 'risk dilution' hypothesis predicts that herring gulls will be *less* neophobic on average when in a group compared to when they are alone (scenario A in [Figure 1](#)). Second, the 'negotiation' hypothesis predicts that individuals will approach novel objects *slower* when in group (scenario B in [Figure 1](#)). Third, according to the 'social conformity' hypothesis, individuals will tend to mimic one another's behaviours—those who are neophobic will show a decrease in their fear of novel objects when surrounded by others who are less neophobic, and vice versa (scenario C in [Figure 1](#)). Thus, in this third scenario, there is a reduction of variance but no change in the average response. These three predictions are contrasted with

the null hypothesis that social context does not modulate variance, or group means ('Null Hypothesis', Figure 1).

To test these predictions, juvenile herring gulls will be subjected to four distinct conditions: individual or group tests paired with a control or novel object. Each condition will be repeated twice. The guidelines for designing neophobia tests of Gregg et al. (2015) were followed, and a within-subject design with a relatively large sample size (N = 80) was chosen to further increase the statistical power of the study. One additional reason for the inconsistent previous findings is that sample size was relatively low in many studies (see also Farrar et al., 2020). In addition, the herring gulls used in this study will be raised by hand from the egg to control for sampling bias, a recurring issue when testing wild animals. After testing, they will be released in the wild.

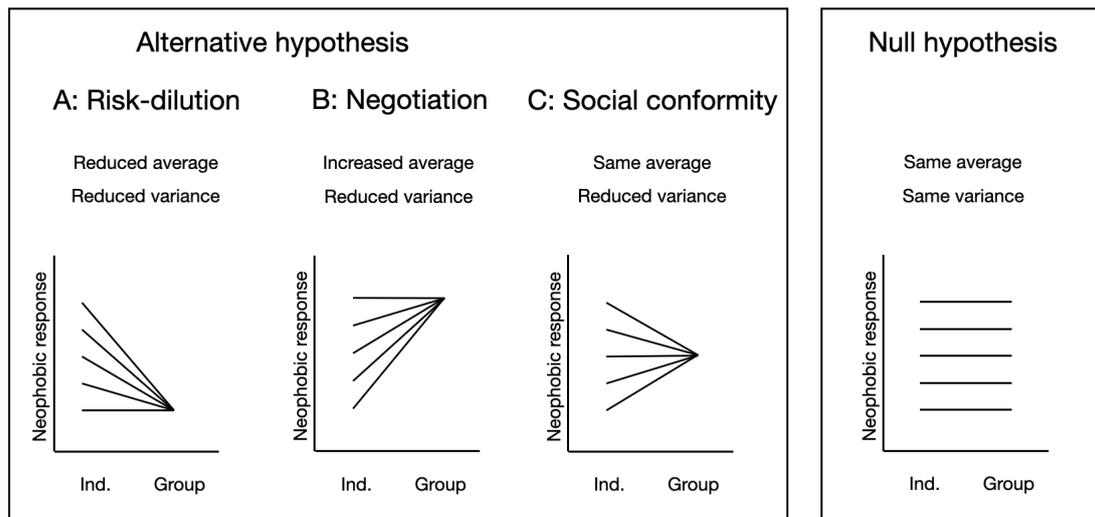


Figure 1. Overview of hypotheses

Material and methods

Sample size

We will test 80* herring gulls twice across a 2x2 design (thus eight tests per individual; see above). We performed an *a-priori* power sensitivity analyses using G*Power (Erdfeider et al., 2009), for a repeated measures MANOVA with three within-subject factors: *Context* (with levels Group and Individual), *Object* (with levels Control and Novel Object), and *Trial* (with levels 1 and 2). Our sample size is sufficient to detect small main effects of *Context*, *Object*, and *Trial* (Cohen's *f* effect size of 0.11 (Cohen, 2013); Power = 0.80 ; cor. among RM = 0.5), as well as an interaction between Context and Object with small effect size (0.11; Power = 0.80 ; cor. among RM = 0.5). Our sensitivity analyses are based on MANOVAs (repeated-measures, within-species factors). However, as discussed below, we will analyse our data with (G)LMMs, which are currently not covered by G*Power or most other power-estimation tools. These mixed-effect models are more flexible in assigning variance as they allow for the specification of both fixed and random effects. By accounting for unexplained variance, our proposed mixed-effect models are more powerful than the fixed-effect MANOVAs used in our sensitivity analyses.

*As gulls are reared from the egg, in a small number of cases (typically less than 10%), herring gull eggs are mistaken for those of the phylogenetically and ecologically related lesser black-backed gull. The species can only be determined after testing (when the individuals are older). Test data from lesser black-backed gulls (if any) will be excluded from subsequent analysis. We conducted a power analysis that accounts for a potential 10% drop-out to

ensure that even with this potential reduction, our study would still have sufficient statistical power (Cohen's f effect size of 0.17) to detect significant effects. 139
140

Subjects 141

Egg Collection and Incubation 142

The herring gulls used in this study are part of a larger research project and are raised and tested at the avian research facilities of Ghent University (Lab number LA1400452), located at the Wildlife Rescue Centre (WRC) in Ostend, Belgium. Eggs are collected in May and June 2024, from nests of roof-breeding parents, by the Agentschap voor Natuur en Bos (ANB) and the gull patrol team, authorised to remove eggs along the Belgian coasts for nuisance prevention. Collected before the pipping stage, the eggs are transported to the WRC under stable conditions for further incubation, using Brinsea Ova-Easy incubators (temperature = 37.5°C; humidity = 45%). Upon arrival eggs are marked with a unique nest identifier and the two largest eggs are incubated. They are checked twice daily for small cracks, indicating pipping. Eggs showing signs of pipping, are moved to a MS700U Hatchery (temperature = 37.2°C; humidity = 50%). 143
144
145
146
147
148
149
150
151

Chick Rearing 152

Once hatched and fully dried, the chicks receive a unique combination of colour rings for identification. The chicks are then housed in groups of 10 in boxes with netting bottoms (size = 120 x 60 x 60cm, LWH) within heated rooms (ambient temperature= 15-25°C; humidity=40%-80%; under natural light conditions). Each box contains a heating plate (30 x 30cm). The semi-precocial chicks are hand-fed small pieces of fish and dog pellets soaked in water, supplemented with Akwavit, a complementary feed specially developed for fish eating animals (Kasper Faunafood, The Netherlands). Food is available *ad libitum*. Once the chicks are at least 5 days old and their weight exceeds 60 grams, they are moved to outside enclosures (size = 500 x 205 x 265cm, LWH), housed in stable groups of 10 individuals. Outside, heating plates are provided during the first few days when night-time temperatures are forecast to drop below 5°C, or in the event of adverse weather conditions such as heavy rain or storms. Food consists of a mixture of dog pellets soaked in water and fish, provided 4 times per day, following the default policy at the WRC. Water is provided *ad libitum*. Individuals are tested when they are approximately 30 days old, shortly before they reach fledging age. After testing, the birds are moved to a large flight cage (approximately 180m²) for dehabitation from handling. Once they are 8-10 weeks old, birds are released in the wild, and a subset (n = 50) receives a GPS-tracker. 153
154
155
156
157
158
159
160
161
162
163
164
165
166

Behavioural Test: Novel Object Task 167

Task Design: For testing purposes, each home enclosure containing ten birds is pseudo-randomly divided into two ~~separate-stable~~ testing groups of five known individuals. This division ensures nestmates are not placed in the same testing group. This arrangement allows to maintain consistent housing conditions when not testing, while facilitating specific configurations during testing sessions. In the 'novel object' condition, birds are exposed to a pseudo-randomly selected novel object (Supp. table 1). Conversely, in the 'control object' condition, a familiar object is placed in the home enclosure for six days prior to testing. By placing a familiar object behind the food plate prior to testing, we can observe responses during testing that are elicited by the novelty of the object and not just the presence of the object itself (see e.g. (Greggor et al., 2015) for justification). ~~Throughout the testing period, the~~ The familiar object remains in place ~~and the novel object is introduced only during the testing sessions,~~ throughout the testing and habituation period to avoid dishabitation from the familiar object. It is replaced by the novel object only during the novel object testing sessions. To preserve the integrity of the experimental design, the novel object introduced in each of the four sessions is unique, thus each bird's interaction with it marks their first encounter. The experimental timeline spans from late June to mid-July, lasting for 8 consecutive days. 168
169
170
171
172
173
174
175
176
177
178
179
180
181

Objects: We will use five **objects** of similar size (approximately the same size as a four weeks old gull), but of different colour, form and texture. 182
183

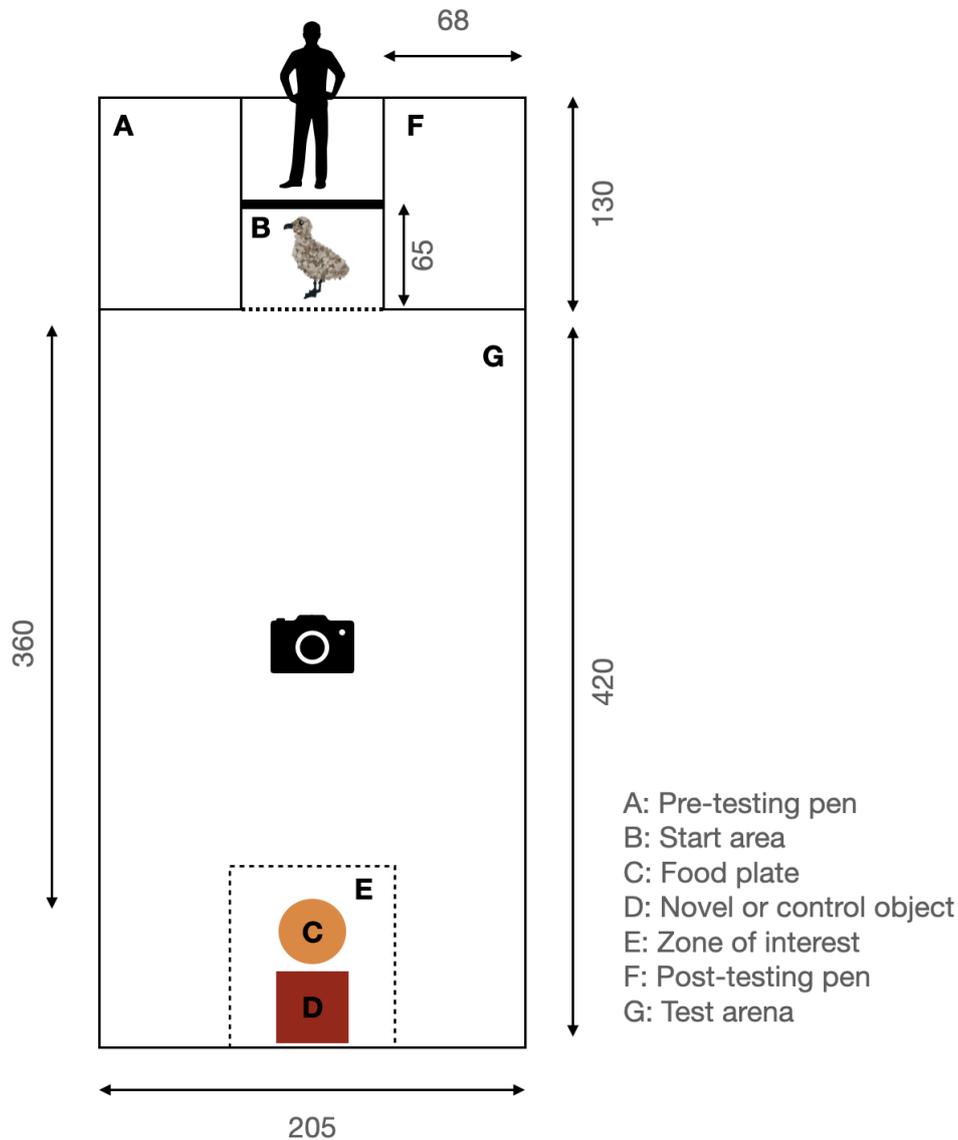


Figure 2. Test setup in home enclosure.

Prior to the Task: In preparation of the novel object task, and following a series of cognitive tests as part of another study (three tests in total), the **test setup** will be introduced into the birds' home enclosure when the birds are not present. This setup includes the pre- and post-testing pens, the start area, and one of our five pseudo-randomly selected **objects**, which will later act as the control object in the neophobia assessments. After having introduced the test setup, birds are allowed to accustom to the presence of the test apparatus for a period of **three six** days. This habituation period minimises any potential stress towards a new environment, which may influence the behavioural outcome of the test trials. 184
185
186
187
188
189
190

In order to distinguish the birds when they are being tested in a group, each individual **will receive is given** a unique marker (**marker pen, Raidex**) a few days before the test, which can be easily detected by a roof-mounted camera, as the colour rings are not visible in the video recordings. " 191
192
193

Testing Protocol: The testing commences after the six-day habituation period. Order of conditions is counterbalanced to incorporate control and novel object conditions, as well as individual versus group settings, with the entire sequence repeated twice. The animals are food deprived since their last feeding moment the 194
195
196



Figure 3. Novel or control objects.

evening before each test at 5:30 PM, to reduce motivational differences before testing. Testing begins at 8:30 AM and is expected to be completed around 11 AM. In both group and individual trials, individuals will have a maximum of 10 minutes for entering the test arena, and an additional 10 minutes to feed, which is consistent with previous novel object studies (Brown and Nemes, 2008; Bruijn and Romero, 2021; Lecuelle et al., 2011). All tests will be recorded with roof-mounted cameras.

Prior to testing, all the birds will be moved to the pre-testing holding pen. Next, a stacked plate of fish and an object (novel or control, depending on the condition) will be placed at the back of the enclosure, with the food plate placed in front of the object to rule out directional preference. A single bird, or group of birds, depending on the social context, will be placed in the start area. The tester will lift the door of the start area after 15 seconds and leave, giving the bird(s) access to their home enclosure (Figure 2). The first 10 minutes start ~~the moment the door starts moving~~ when the door begins to move, the second 10 minutes start ~~once all individuals left the start box. The testing session ends once all birds interact with the food, or once for each bird individually when it leaves the start area. The test session ends~~ 10 minutes ~~have passed~~ after the bird has left the start area. Next, the tester moves the tested bird(s) to the post-testing holding pen and starts a new test with a new (group of) bird(s).

Data processing and analysis

Video coding. We will code all videos using the free, open-source software BORIS (Behavioural Observation Research Interactive Software) (Friard and Gamba, 2016). We will code four events, namely 'start of trial', 'test arena entry', 'eating', and 'zone of interest' (see Table 1 for full descriptions). Based on the coded events, we will determine latencies and cumulative times. By extracting the time difference between 'start of trial' and 'test arena entry', we will determine the latency to leave the start area (Figure 2). In order to determine the latency to approach the food, we will extract the time difference between 'test arena entry' and 'eating'. Time

spent in the zone of interest (i.e. in proximity to the food reward and/or novel object, see [Figure 2](#)) is calculated as the cumulative time over the length of the trial. If an individual does not perform a specific behaviour, we will assign the maximum latency, meaning the full task duration (in seconds), to that behaviour. For example, the behaviour 'test arena entry' will have a latency of 600 seconds if an individual does not enter the test arena. For the group tests, we will follow each bird individually to code their behaviours.

Video coding will be a shared task between multiple experimenters, with 20 percent of all videos being double-coded to assess inter-rater-reliability (IRR) using Cohen's Kappa. We aim for $0.81 \leq \text{Cohen's Kappa} \leq 1.0$, which indicates strong to almost perfect agreement between coders (McHugh, 2012). If we will have a Cohen's Kappa below this value, we will assess each behaviour individually to determine which behaviours need to be recoded for all videos.

Table 1. Ethogram of behaviours that will be coded in BORIS. The 'Zone of interest' is defined as a fixed rectangle that includes the object and the food bowl. To ensure comprehensive observation coverage, this area is expanded by the approximate body length of a 4-week-old gull (30 cm). This ensures that all relevant activities within and around the novel object are captured.

Action	Definition
Start of trial (Point event)	Moment the door starts moving.
Test arena entry (Point event)	When the entire bird is outside the start area.
Eating (Point event)	When the beak touches the food.
Zone of interest (State event)	When the front half of the bird crosses the (notional) line.

Statistical analysis Statistical analyses will be conducted using R, version 4.3.X (R Core Team, 2021). Mixed-Effects Models (MMs), either linear MMs (LMMs) or generalised LMMs (GLMMs), will be fitted using the `lme4` package (Bates et al., 2015). For LLMs, parameter estimation and p-values for the estimated models will be calculated by means of the `lmerTest` package (Kuznetsova et al., 2017) via the the Satterthwaite's degrees of freedom method; for GLMMs, the `car` (Fox and Weisberg, 2019) or `carData` (Fox, Weisberg, and Price, 2022) package will be used. For the GLMM, we will use partial η -squared (η_p^2) as effect sizes, and they will be calculated by means of the `r2glmm` (Jaeger, 2017) package. Models will be fitted to the different latency measures separately, as well as combined. For the combined analysis, the approach proposed by Snijders and Bosker, 2012 will be used, which allows for the simultaneous analysis of multiple dependent variables in the case of nested data structures, thereby considering within-group and between-group variance in latency measures.

As we aim to determine whether the average neophobic response differs between individual and group trials, a (G)LMM with Type III sum of squares will be performed on the latency measures ([Table 1](#)). This analysis will include both fixed and random effects to explore the impact of different experimental conditions. The model will incorporate *Object*, *Context*, and their interaction as key fixed effects to explore how the type of object and the social setting (alone vs. in a group) interactively affect latency responses. Additionally, *Trial* will be included as a fixed effect to control for the impact of trial repeat. To specifically assess the variability in latency across individual and group trials, we will compare the estimated variance components within our mixed-effects model. Variance for individual trials will be estimated from the *Indiv_Dummy* effect at the BirdID level. For group trials, the combined estimated variances of the *Group_Dummy* effect at both the BirdID and GroupID levels will be evaluated. This comparison aims to determine whether individual differences are more pronounced in solitary compared to group settings, with an expectation that individual variances and the total variance might be higher in individual trials. Additionally, an analysis at the BirdID level between the estimated variances of the *Indiv_Dummy* and *Group_Dummy* effects will further elucidate how individual differences manifest under different trial conditions, potentially highlighting the influence of group dynamics on individual behaviour.

$$\begin{aligned}
& \text{Latency} \sim, \text{Object} \times \text{Context} + \text{Trial} \\
& + (1|\text{NestID}) \\
& + (-1 + \text{Group_Dummy}|\text{GroupID}) \\
& + (-1 + \text{Indiv_Dummy} + \text{Group_Dummy}|\text{BirdID})
\end{aligned}$$

In the model, *Object* refers to the stimulus presented, distinguishing between control and novel objects. *Trial* captures the two testing sessions conducted, and *Context* indicates the social environment, differentiating between individual and group settings. Random effects structures are tailored to accurately reflect the individual and group-level variability in responses. Specifically, *NestID* is included to control for similarities within nests, *Group_Dummy* identifies trials conducted in group setting, effectively marking the presence of social interactions during the test. Conversely, *Indiv_Dummy* indicates the absence of such group dynamics, highlighting trials where subjects are tested alone.

In all instances, model plots will be generated using the `performance` package (Lüdtke et al., 2021) to inspect violations of model assumptions, such as heteroscedasticity, non-normality of residuals, and the presence of outliers. Multicollinearity and autocorrelation will be evaluated, with potential model adjustments including transformation of variables or modification of the model structure (e.g., switching from LMM to GLMM). In terms of model design, binary predictors will be encoded using contrast coding (-0.5 vs. 0.5), optimizing the interpretability and efficiency of our analyses in the context of our perfectly balanced predictor variables. Post-hoc analyses, following significant findings, will be performed with Bonferroni-Holm corrected contrasts to further explore the data. Given the balanced nature of our model predictors, concerns related to multicollinearity are minimised, negating the need for variance inflation factor (VIF) assessments traditionally used to identify redundancy among predictors.

Discussion

Appendices

These are your appendices

Acknowledgements

This is your acknowledgments.

Fundings

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

Data, script, code, and supplementary information availability

All necessary data, scripts, and code required to replicate our study's findings will be made openly accessible at the article's [OSF repository](#). Supplementary information, supporting our results, will also be made available at this repository.

References

- 286
- Apfelbeck B and M Raess (2008). Behavioural and hormonal effects of social isolation and neophobia in a 287
gregarious bird species, the European starling (*Sturnus vulgaris*). *Hormones and Behavior* 54, 435–441. ISSN: 288
0018506X. <https://doi.org/10.1016/j.yhbeh.2008.04.003>. 289
- Bates D, M Mächler, BM Bolker, and SC Walker (Oct. 2015). Fitting Linear Mixed-Effects Models Using lme4. 290
Journal of Statistical Software 67 (1), 1–48. ISSN: 1548-7660. <https://doi.org/10.18637/JSS.V067.I01>. 291
- Benson-Amram S and KE Holekamp (2012). Innovative problem solving by wild spotted hyenas. *Proceedings* 292
of the Royal Society B: Biological Sciences 279, 4087–4095. ISSN: 0962-8452, 1471-2954. [https://doi.org/10.](https://doi.org/10.1098/rspb.2012.1450) 293
[1098/rspb.2012.1450](https://doi.org/10.1098/rspb.2012.1450). 294
- Biondi LM, MS Bó, and AI Vassallo (2010). Inter-individual and age differences in exploration, neophobia and 295
problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Animal cognition* 13, 701–710. <https://doi.org/10.1007/s10071-010-0319-8>. 296
[//doi.org/10.1007/s10071-010-0319-8](https://doi.org/10.1007/s10071-010-0319-8). 297
- Both C, NJ Dingemanse, PJ Drent, and JM Tinbergen (July 2005). Pairs of extreme avian personalities have 298
highest reproductive success. *Journal of Animal Ecology* 74 (4), 667–674. ISSN: 00218790. [https://doi.org/](https://doi.org/10.1111/j.1365-2656.2005.00962.x) 299
[10.1111/j.1365-2656.2005.00962.x](https://doi.org/10.1111/j.1365-2656.2005.00962.x). 300
- Brown GR and C Nemes (July 2008). The exploratory behaviour of rats in the hole-board apparatus: Is head- 301
dipping a valid measure of neophilia? *Behavioural Processes* 78 (3), 442–448. ISSN: 0376-6357. [https://doi.](https://doi.org/10.1016/j.BEPROC.2008.02.019) 302
[org/10.1016/j.BEPROC.2008.02.019](https://doi.org/10.1016/j.BEPROC.2008.02.019). 303
- Bruijn R de and LM Romero (Feb. 2021). Chronic stress reverses enhanced neophobia following an acute 304
stressor in European starlings. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 305
335 (2), 265–274. ISSN: 2471-5646. <https://doi.org/10.1002/JEZ.2431>. 306
- Cohen J (2013). *Statistical power analysis for the behavioral sciences*. Routledge. 307
- Coleman SL and RL Mellgren (1994). Neophobia when feeding alone or in flocks in zebra finches, *Taeniopygia* 308
guttata. *Animal Behaviour* 48, 903–907. <https://doi.org/https://doi.org/10.1006/anbe.1994.1315>. 309
- Coulson JC (2015). Re-Evaluation of the Role of Landfills and Culling in the Historic Changes in the Herring Gull 310
(*Larus argentatus*) Population in Great Britain. *Waterbirds* 38, 339–354. [https://doi.org/https://doi.org/10.](https://doi.org/https://doi.org/10.1675/063.038.0411) 311
[1675/063.038.0411](https://doi.org/https://doi.org/10.1675/063.038.0411). 312
- Erdfelder E, F FAul, A Buchner, and AG Lang (2009). Statistical power analyses using G*Power 3.1: Tests for 313
correlation and regression analyses. *Behavior Research Methods* 41 (4), 1149–1160. ISSN: 1554351X. [https://doi.org/](https://doi.org/10.3758/BRM.41.4.1149/METRICS) 314
[//doi.org/10.3758/BRM.41.4.1149/METRICS](https://doi.org/10.3758/BRM.41.4.1149/METRICS). 315
- Farrar B, M Boeckle, and N Clayton (2020). Replications in Comparative Cognition: What Should We Expect and 316
How Can We Improve? *Animal Behavior and Cognition* 7, 1–22. ISSN: 23725052, 23724323. [https://doi.org/](https://doi.org/10.26451/abc.07.01.02.2020) 317
[10.26451/abc.07.01.02.2020](https://doi.org/10.26451/abc.07.01.02.2020). 318
- Feist F, K Smith, and P Graham (May 2023). Inter-species stimulus enhancement: herring gulls (*Larus argentatus*) 319
mimic human food choice during foraging. *Biology Letters* 19 (5). ISSN: 1744957X. [https://doi.org/10.1098/](https://doi.org/10.1098/RSBL.2023.0035) 320
[RSBL.2023.0035](https://doi.org/10.1098/RSBL.2023.0035). 321
- Fox J and S Weisberg (2019). *An R Companion to Applied Regression*. Third. Thousand Oaks CA: Sage. 322
- Fox J, S Weisberg, and B Price (2022). *carData: Companion to Applied Regression Data Sets*. 323
- Friard O and M Gamba (May 2016). BORIS: A free, versatile open-source event-logging software for video/audio 324
coding and live observations. *Methods in Ecology and Evolution* 7. <https://doi.org/10.1111/2041-210X.12584>. 325
- Frings H, M Frings, B Cox, and L Peissner (1955). Auditory and visual mechanisms in food-finding behavior of 326
the Herring Gull. *The Wilson Bulletin*, 155–170. <https://doi.org/10.2307/4158412>. 327
- Gandolfi G (2009). Gilberto Gandolfi (1975) Social learning in non-primate animals. *Italian Journal of Zoology* 42 328
(4), 311–329. ISSN: 0373-4137. <https://doi.org/10.1080/11250007509431449>. 329
- Gao J and BC O'Neill (May 2020). Mapping global urban land for the 21st century with data-driven simulations 330
and Shared Socioeconomic Pathways. *Nature Communications* 11, 2302. ISSN: 2041-1723. [https://doi.org/](https://doi.org/10.1038/s41467-020-15788-7) 331
[10.1038/s41467-020-15788-7](https://doi.org/10.1038/s41467-020-15788-7). 332

- Goumas M, NJ Boogert, and LA Kelley (Feb. 2020). Urban herring gulls use human behavioural cues to locate food. *Royal Society Open Science* 7 (2). ISSN: 20545703. <https://doi.org/10.1098/RSOS.191959>.
- Greenberg R (2003). The Role of Neophobia and Neophilia in the Development of Innovative Behaviour of Birds. In: *Animal Innovation*. Ed. by Reader SM and Laland KN. Oxford University Press, pp. 175–196.
- Greenberg R and C Mettke-Hofmann (Jan. 2001). Ecological Aspects of Neophobia and Neophilia in Birds. *Current Ornithology* 16. https://doi.org/https://doi.org/10.1007/978-1-4615-1211-0_3.
- Greggor AL, A Thornton, and NS Clayton (Dec. 2015). Neophobia is not only avoidance: improving neophobia tests by combining cognition and ecology. *Current Opinion in Behavioral Sciences* 6, 82–89. ISSN: 2352-1546. <https://doi.org/10.1016/j.COBEGA.2015.10.007>.
- Griffin AS, F Lermite, M Perea, and D Guez (2013). To innovate or not: contrasting effects of social groupings on safe and risky foraging in Indian mynahs. *Animal Behaviour* 86, 1291–1300. ISSN: 00033472. <https://doi.org/10.1016/j.anbehav.2013.09.035>.
- Harel R, O Spiegel, WM Getz, and R Nathan (Apr. 2017). Social foraging and individual consistency in following behaviour: testing the information centre hypothesis in free-ranging vultures. *Proceedings of the Royal Society B: Biological Sciences* 284 (1852). ISSN: 1471-2954. <https://doi.org/10.1098/RSPB.2016.2654>.
- Herbert-Read JE, S Krause, LJ Morrell, TM Schaerf, J Krause, and AJW Ward (2013). The role of individuality in collective group movement. *Proceedings of the Royal Society B: Biological Sciences* 280, 20122564. <https://doi.org/10.1098/rspb.2012.2564>.
- Inzani EL, LA Kelley, and NJ Boogert (2023). Object neophilia in wild herring gulls in urban and rural locations. *Journal of Avian Biology* 2023, e03028. ISSN: 0908-8857, 1600-048X. <https://doi.org/10.1111/jav.03028>.
- Jaeger B (2017). *r2glmm: Computes R Squared for Mixed (Multilevel) Models*. R package version 0.1.2.
- Kareklas K, RW Elwood, and RA Holland (2018). Grouping promotes risk-taking in unfamiliar settings. *Behavioural Processes* 148, 41–45. ISSN: 03766357. <https://doi.org/10.1016/j.beproc.2018.01.003>.
- Keen SC, EF Cole, MJ Sheehan, and BC Sheldon (Feb. 2020). Social learning of acoustic anti-predator cues occurs between wild bird species. *Proceedings of the Royal Society B* 287 (1920). ISSN: 14712954. <https://doi.org/10.1098/RSPB.2019.2513>.
- Kelly TR, MG Kimball, KR Stansberry, and CR Lattin (2020). No, you go first: phenotype and social context affect house sparrow neophobia. *Biology Letters* 16, 20200286. ISSN: 1744-9561, 1744-957X. <https://doi.org/10.1098/rsbl.2020.0286>.
- Kerman K, KE Sieving, CS Mary, and ML Avery (2018). Social conformity affects experimental measurement of boldness in male but not female monk parakeets (*Myiopsitta monachus*). *Behaviour* 155, 1025–1050. <https://doi.org/10.1163/1568539X-00003519>.
- Kikusui T, JT Winslow, and Y Mori (2006). Social buffering: relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361, 2215–2228. ISSN: 0962-8436, 1471-2970. <https://doi.org/10.1098/rstb.2006.1941>.
- Kimball M and C Lattin (Jan. 2023). The "Seven Deadly Sins" of Neophobia Experimental Design. *SSRN Electronic Journal*. <https://doi.org/10.2139/ssrn.4511040>.
- King AJ, LJ Williams, and C Mettke-Hofmann (2015). The effects of social conformity on Gouldian finch personality. *Animal Behaviour* 99, 25–31. <https://doi.org/10.1016/j.anbehav.2014.10.016>.
- Krause J and G Ruxton (2002). *Living in Groups*. Oxford University Press, USA. ISBN: 0198508174.
- Kuznetsova A, PB Brockhoff, and RH Christensen (Dec. 2017). ImerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software* 82 (13), 1–26. ISSN: 1548-7660. <https://doi.org/10.18637/JSS.V082.I13>.
- Lecuelle S, I Bouvarel, AM Chagneau, F Laviro, P Lescoat, and C Leterrier (Jan. 2011). Early visual experience of food does not appear to reduce subsequent feed neophobia in turkeys. *Poultry Science* 90 (1), 1–9. ISSN: 0032-5791. <https://doi.org/10.3382/PS.2010-00882>.
- Lee VE and A Thornton (Mar. 2021). Animal Cognition in an Urbanised World. *Frontiers in Ecology and Evolution* 9, 633947. ISSN: 2296701X. <https://doi.org/10.3389/FEVO.2021.633947/BIBTEX>.

- Loukola OJ, JT Seppänen, and JT Forsman (Mar. 2012). Intraspecific social information use in the selection of nest site characteristics. *Animal Behaviour* 83 (3), 629–633. ISSN: 0003-3472. <https://doi.org/10.1016/j.anbehav.2011.12.004>. 380
- Lüdecke D, MS Ben-Shachar, I Patil, P Waggoner, and D Makowski (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software* 6, 3139. <https://doi.org/10.21105/joss.03139>. 381
- McHugh M (Oct. 2012). Interrater reliability: The kappa statistic. *Biochemia medica : časopis Hrvatskoga društva medicinskih biokemičara / HDMB* 22, 276–82. <https://doi.org/10.11613/BM.2012.031>. 382
- McKinney ML (Oct. 2002). Urbanization, Biodiversity, and Conservation: The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience* 52, 883–890. ISSN: 0006-3568. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2). 383
- Mettke-Hofmann C (2017). Neophobia. In: *Encyclopedia of Animal Cognition and Behavior*. Ed. by Vonk J and Shackelford T. Cham: Springer International Publishing, pp. 1–8. ISBN: 978-3-319-47829-6. https://doi.org/10.1007/978-3-319-47829-6_908-1. 384
- Mettke-Hofmann C, H Winkler, and B Leisler (2002). The Significance of Ecological Factors for Exploration and Neophobia in Parrots. *Ethology* 108, 249–272. ISSN: 0179-1613, 1439-0310. <https://doi.org/10.1046/j.1439-0310.2002.00773.x>. 385
- Miller R, T Bugnyar, K Pölzl, and C Schwab (2015). Differences in exploration behaviour in common ravens and carrion crows during development and across social context. *Behavioral Ecology and Sociobiology* 69, 1209–1220. ISSN: 0340-5443, 1432-0762. <https://doi.org/10.1007/s00265-015-1935-8>. 386
- Miller R, ML Lambert, A Frohnwieser, KF Brecht, T Bugnyar, I Crampton, E Garcia-Pelegrin, K Gould, AL Greggor, El Izawa, et al. (2022). Socio-ecological correlates of neophobia in corvids. *Current Biology* 32, 74–85. <https://doi.org/https://doi.org/10.1016/j.cub.2021.10.045>. 387
- Moretti L, M Hentrup, K Kotrschal, and F Range (2015). The influence of relationships on neophobia and exploration in wolves and dogs. *Animal Behaviour* 107, 159–173. <https://doi.org/10.1016/j.anbehav.2015.06.008>. 388
- Nager RG and NJ O'Hanlon (Apr. 2016). Changing Numbers of Three Gull Species in the British Isles. *Waterbirds* 39 (sp1), 15–28. ISSN: 15244695. <https://doi.org/10.1675/063.039.SP108>. 389
- O'Hanlon NJ, RA McGill, and RG Nager (July 2017). Increased use of intertidal resources benefits breeding success in a generalist gull species. *Marine Ecology Progress Series* 574, 193–210. ISSN: 0171-8630. <https://doi.org/10.3354/MEPS12189>. 390
- Pavlova O and T Wronski (May 2020). City gulls and their rural neighbours: Changes in escape and agonistic behaviour along a rural-to-urban gradient. In: Nova Science Publishers, Inc. ISBN: 978-1-53618-000-8. 391
- R Core Team (2021). R: A Language and Environment for Statistical Computing. 392
- Schuetz W and S Dall (Feb. 2009). Sex differences, social context and personality in Zebra Finches, *Taeniopygia guttata*. *Animal Behaviour* 77, 1041–1050. <https://doi.org/10.1016/j.anbehav.2008.12.024>. 393
- Snijders TAB and RJ Bosker (2012). *Multilevel analysis : an introduction to basic and advanced multilevel modeling*. 2nd ed. Los Angeles ; London : SAGE. ISBN: 9781849202008; 1849202001; 9781849202015; 184920201X. 394
- Soma M and T Hasegawa (2004). The Effect of Social Facilitation and Social Dominance on Foraging Success of Budgerigars in an Unfamiliar Environment. *Behaviour* 141, 1121–1134. ISSN: 0005-7959, 1568-539X. <https://doi.org/10.1163/1568539042664560>. 395
- St. Lawrence S, I Rojas-Ferrer, and J Morand-Ferron (2021). Does the presence of a conspecific increase or decrease fear? Neophobia and habituation in zebra finches. *Ethology* 127, 1033–1041. ISSN: 0179-1613, 1439-0310. <https://doi.org/10.1111/eth.13224>. 396
- Stöwe M, T Bugnyar, B Heinrich, and K Kotrschal (2006). Effects of Group Size on Approach to Novel Objects in Ravens (*Corvus corax*). *Ethology* 112, 1079–1088. ISSN: 0179-1613, 1439-0310. <https://doi.org/10.1111/j.1439-0310.2006.01273.x>. 397

Stöwe M, T Bugnyar, MC Loretto, C Schloegl, F Range, and K Kotrschal (2006). Novel object exploration in ravens (*Corvus corax*): Effects of social relationships. *Behavioural Processes* 73, 68–75. ISSN: 03766357. <https://doi.org/10.1016/j.beproc.2006.03.015>. 427
428
429

Vernouillet A and DM Kelly (2020). Individual exploratory responses are not repeatable across time or context for four species of food-storing corvid. *Scientific Reports* 10, 394. <https://doi.org/10.1038/s41598-019-56138-y>. 430
431
432

Vrublevska J, T Krama, MJ Rantala, P Mierauskas, TM Freeberg, and IA Krams (June 2015). Personality and density affect nest defence and nest survival in the great tit. *Acta Ethologica* 18 (2), 111–120. ISSN: 08739749. <https://doi.org/10.1007/S10211-014-0191-7/FIGURES/3>. 433
434
435

Supplementary material 436

Supplementary Table 1: Neophobia testing schedule

Note: "GC" signifies Group Control, "IC" indicates Individual Control, "GT" represents Group Test, and "IT" stands for Individual Test. The subsequent number (1 or 2) specifies whether it is the first instance or a repeat. The suffix "-X" identifies the specific object involved, numbers 1-5 corresponding to randomly assigned novel or control objects.

Day/Cage	Cage 1	Cage 2	Cage 3	Cage 4	Cage 5	Cage 6	Cage 7	Cage 8
Day 1	GC1 - 1	IC1 - 2						
Day 2	IC1 - 1	GT1 - 4						
Day 3	GT1 - 4	IT1 - 1						
Day 4	IT1 - 3	GC1 - 2	GT1 - 5	IT1 - 1				
Day 5	GC2 - 1	IC2 - 2	IT1 - 1	GC1 - 4				
Day 6	IC2 - 1	GT2 - 5	GC1 - 3	IC1 - 4				
Day 7	GT2 - 2	IT2 - 3	IC1 - 3	GT1 - 3	GC1 - 1	IC1 - 2		
Day 8	IT2 - 5	GC2 - 2	GT2 - 4	IT2 - 2	IC1 - 1	GT1 - 3		
Day 9			IT2 - 2	GC2 - 4	GT1 - 2	IT1 - 4		
Day 10			GC2 - 3	IC2 - 4	IT1 - 3	GC1 - 2	GT1 - 2	IT1 - 1
Day 11			IC2 - 3	GT2 - 5	GC2 - 1	IC2 - 2	IT1 - 4	GC1 - 4
Day 12					IC2 - 1	GT2 - 5	GC1 - 3	IC1 - 4
Day 13					GT2 - 4	IT2 - 1	IC1 - 3	GT1 - 5
Day 14					IT2 - 5	GC2 - 2	GT2 - 1	IT2 - 2
Day 15							IT2 - 5	GC2 - 4
Day 16							GC2 - 3	IC2 - 4
Day 17							IC2 - 3	GT2 - 3

Question	Hypothesis	Sampling plan	Analysis Plan	Rationale for deciding the sensitivity of the test for confirming or disconfirming the hypothesis	Interpretation given different outcomes	Theory that could be shown wrong by the outcomes
<p>Does the individual degree of neophobia differ across social contexts in a highly social species, the herring gull?</p>	<p>We hypothesise that the distribution of neophobic responses will change in a group context.</p> <p>Specifically:</p> <p>a.) There is a reduction of the variance in group tests.</p> <p>b.) The average response differs between group/individual tests, depending on the social mechanism at play</p>	<p>We will test 80 herring gulls twice across a 2x2 design. These four distinct conditions are: individual or group tests paired with a control or novel object. Each condition will be repeated twice. In the 'novel object' condition, birds are exposed to a pseudo-randomly selected novel object. Conversely, the 'control object' condition involves a familiar object, previously placed in their home enclosure for six days before testing. Testing trials will be randomised, see Supplementary table 1 in the main manuscript</p>	<p>A (G)LMM with Type III sum of squares will be performed on the different latency measures. Models will be fitted to the different latency types separately as well as combined. For the combined analysis, we will use the approach proposed by Snijders and Boskers (2012), which allows for the simultaneous analysis of multiple dependent variables in the case of nested data structures, thereby</p>	<p><i>A-priori</i> power sensitivity analyses were conducted in G*Power (Erdfeiler et al., 2009), using a MANOVA. This indicated that our sample size of 80 animals is sufficient to detect a small effect of <i>Context, Group and Trial</i>. However, we will analyse our data with (G)LMMs, which are currently not covered by G*Power or most other power-estimation tools. These models are</p>	<p>If social context fails to modulate variance, or group means, it could suggest that social contexts hold little significance for neophobic responses among herring gulls.</p>	<p>Social context may either modulate the group mean, the variance, or both. The risk dilution hypothesis suggests that being in a group will reduce both the mean and the variance of neophobia. Conversely, the negotiation hypothesis predicts an increase in mean neophobia but a decrease in within-group variance. The social conformity hypothesis predicts no change</p>

		<p>for a detailed testing schedule.</p> <p>Testing groups comprise 5 individuals by semi-randomly allocating gulls to one group. We will split nest mates across groups. Sexing is unfeasible prior to testing. While we will consider sex differences in our statistical analyses, we do not expect an effect of sex since herring gulls only reach sexual maturity at 4-years of age. Groups may also include a lesser black-backed gull. We will include all gulls for testing but will remove the lesser black-backed gulls prior to conducting the statistical analysis.</p>	<p>considering within-group and between-group variance in latency measures.</p> <p>The model will incorporate <i>Object</i>, <i>Context</i>, their interaction and <i>Trial</i> as fixed effect.</p> <p>A random slope for <i>Group</i> associated with each <i>GroupID</i> will be included focusing on the variability of the group effect. Moreover, the variability in the individual response due to being in a group or not will be modelled as random effects within <i>BirdID</i>.</p>	<p>more flexible in assigning variance as they allow for the specification of both fixed and random effects. However, by accounting for unexplained variance, our proposed mixed-effect models are more powerful than the fixed-effect MANOVAs used in our sensitivity analyses.</p>		<p>in mean neophobia, but a decrease in variance. The design of our study allows us to validate or refute each of these hypotheses.</p>
--	--	---	--	--	--	---