

Socio-ecological correlates of neophobia in corvids

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Summary

Behavioural responses to novelty, including fear and subsequent avoidance of novel stimuli, i.e. neophobia, determine how animals interact with their environment. Neophobia aids in navigating risk and impacts on adaptability and survival. There is variation within and between individuals and species, however, lack of large-scale, comparative studies critically limits investigation of the socio-ecological drivers of neophobia. In this study, we tested responses to novel objects and food (alongside familiar food) versus a baseline (familiar food alone) in 10 corvid species (241 subjects) across 10 labs worldwide. There were species differences in the latency to touch familiar food in the novel object and novel food conditions relative to the baseline. Four of seven socio-ecological factors influenced object neophobia: 1) use of urban habitat (vs not), 2) territorial pair vs family group sociality, 3) large vs small maximum flock size, and 4) moderate vs specialised caching (whereas range, hunting live animals, and genus did not); while only maximum flock size influenced food neophobia. We found that, overall, individuals were temporally and contextually repeatable (i.e. consistent) in their novelty responses in all conditions, indicating neophobia is a stable behavioural trait. With this study, we have established a network of corvid researchers, demonstrating potential for further collaboration to explore the evolution of cognition in corvids and other bird species. These novel findings enable us, for the first time in corvids, to identify the socio-ecological correlates of neophobia and grant insight into specific elements that drive higher neophobic responses in this avian family group.

Keywords

Neophobia, corvids, socio-ecological drivers, repeatability, novelty, species differences

Introduction

Novelty is a common and vital aspect of animal life. The discovery of novel items and environments offers individuals an opportunity to benefit from new resources, such as food, tools, and shelter ^{1,2}. Animals navigate novel stimuli through exploration, which allows for the assessment of any potential utility ^{3,4}. However, novelty also presents the potential for danger: unknown food may be toxic, unknown objects may be traps and unfamiliar species may be predators ¹. Consequently, various species show fear and subsequent avoidance of novel stimuli, otherwise known as neophobia ^{1,5}. Neophobia acts as a protective behaviour, encouraging hesitance and vigilance before/during exploration and thus helps to limit the danger associated with novelty ¹. An appropriate species level of neophobia, according to their niche, should maximise opportunity whilst minimising risk, and is context-specific ⁶. As neophobia affects how animals interact with commonly occurring novelty, an understanding of neophobia is vital for animal cognition and behaviour research. This is particularly relevant as the world becomes heavily urbanised, with many species having to adjust to human-generated environmental changes and the inevitable novelty that follows ⁷. Understanding neophobia from an ontogenetic and evolutionary perspective provides important insight into why some species are more successful in adapting to new environments than others ^{8,9}.

Previous research has investigated factors influencing neophobia, with inter- and intra-specific variation of neophobia (e.g. parrots ¹⁰ and ungulates ¹¹). For example, in 10 ungulate species (78 subjects), neophobia was higher in more socially integrated individuals than less integrated ones, while rank and sex had no effect ¹¹. The extent that wider socio-ecological factors affect the costs and benefits of neophobia is still unknown ¹. Moreover, there are very few large-scale comparative studies of novelty responses. One notable exception is Mettke-Hofmann et al. (2002) on the relationship between ecological factors, including diet and habitat, and neophobia (latency to eat familiar food in presence of novel object) and exploration (latency to touch a novel object) behaviour in 61 parrot species ¹⁰. The results suggested that species' ecology is closely associated with novelty responses. Two factors influenced neophobia: parrots with a diet of insects were more neophobic than those feeding on plant material, explained as a possible consequence of the toxicity danger associated with insects ¹⁰. Thus, increased neophobia may mediate some of this risk. Several variables influenced exploration, such as diet, habitat and island living ¹⁰. We note that this study did not test for individual

94 repeatability, used primarily small sample sizes (range 1-23 individuals, mean = 4.4, median = 2.5),
95 and largely tested in uncontrolled social settings (e.g. a varying number of conspecifics present)¹⁰.

96 Many smaller-scale studies have investigated individual ecological factors on neophobia within
97 species. For example, common myna birds (*Acridotheres tristis*) who inhabit urban environments
98 demonstrate lower levels of neophobia than those from rural areas and are quicker to utilise novel
99 food resources¹². Greggor et al. (2016) found that wild birds (five corvid species, seven other bird
100 species) approached human litter objects faster in an urban environment than in a rural environment
101¹³. These findings have been suggested to occur due to habituation: birds in urban areas encounter
102 human-made items more frequently than those in rural areas and thus become accustomed to this
103 particular type of novelty. Other explanations focus on how urban areas offer low-risk and high-
104 benefit environments, with a vast array of food resources in the form of human litter, and low levels
105 of predation¹⁴⁻¹⁶.

106 Differing habitats and diets may also influence neophobia. The Neophobia Threshold Hypothesis
107 posits that the costs of neophobia outweigh the benefits for generalist species, who utilise a range of
108 resources that vary in availability, so reduced neophobia would enable faster exploration and
109 discovery of new resources^{1,17} (although neophobia and exploration are derived from separate
110 motivations¹). Meanwhile, specialist species, who use fewer, more stable resources, should show
111 greater levels of neophobia as they have limited need to explore new food sources. This has been
112 supported by research indicating that generalist Lesser-Antillean Bullfinch (*Loxigalla noctis*) showed
113 shorter latencies to approach novel feeding stations than specialist bananaquit (*Coereba flaveola*)¹⁸.
114 Similarly, generalist song sparrows (*Melospiza melodia*) were less object neophobic than specialist
115 swamp sparrows (*Melospiza georgiana*) in the field and lab^{17,19}. Alternatively, the Dangerous Niche
116 Hypothesis suggests that neophobia functions to reduce risk, and thereby varies according to the
117 danger level of an animal's particular niche (e.g. risk of predation or food toxicity). For example,
118 some fish and amphibian species show higher levels of neophobia as predation risk increases (²⁰; see
119 also ^{21,22} for related bird studies).

120 Furthermore, social context, like presence of conspecifics, has been shown to reduce neophobia
121 and increase exploration in several species, which could have consequences for species with larger

social groups. For example, zebra finches (*Taeniopygia guttata*) showed shorter latencies to eat from a novel feeder when in a flock than when alone, which may be due to group presence reducing generalised fear and/or risk being shared, thus reducing neophobia²³. This social effect may also be context specific. For instance, Stöwe et al. (2006) found common ravens (*Corvus corax*) approached novel objects faster in the presence of siblings than non-siblings²⁴. Chiarati et al. (2012) found that dominant breeding males in kin-based groups of carrion crows (*Corvus corone corone*) approached novel food before other family members, reducing risks for their partner and offspring²⁵. Among dogs and wolves, individuals spent longer exploring novel objects in the presence of conspecifics than alone²⁶. Similarly, capuchin monkeys, gerbils, and rats, among others, were more likely to accept a novel food if other conspecifics were present or had handled the food^{27–30}.

Individual differences in neophobia and exploration have been shown to be stable traits (i.e. repeatable or consistent over time and contexts) in some species, though inconsistent in others, which may be influenced by a range of factors, including the species, task, measures used, as well as seasonality, developmental, and social influences^{10,25,31–34}. Consistent methodology within a multi-species study allows for effective comparison within and between species³⁵, and thus contributes towards understanding the mechanisms and influences of neophobia.

As a behavioural trait that dictates much of an animal's interaction with the environment, including how they approach and solve novel problems, such data are valuable for establishing links between behaviour and ecology as well as for studying cognition. For instance, the time taken to learn a foraging task in feral pigeons (*Columba livia*) and zenaida doves (*Zenaida aurita*) covaried with individual levels of neophobia³⁶. Indeed, variation in neophobia presents a potential confound for cognition research, as it can impact performance during comparative cognitive tests. However, most comparative cognition studies do not measure neophobia and thus do not control for it statistically³⁷. These studies often incorporate habituation (e.g. with experimental apparatuses) prior to testing as a means of reducing potential neophobia effects. However, it is unclear whether these procedures to reduce neophobia are effective (and equally effective for all species tested). Outside of basic (i.e. knowledge/ curiosity driven) research, neophobia data may help inform applied animal welfare and

conservation, including pre-release training used during reintroduction programmes^{38,39}. For instance, working to increase neophobia levels in animals subjected to culling due to conflict with farmers³⁸.

Corvids (members of crow family) are often featured in cognitive research⁴⁰, and are known to be highly neophobic^{2,41}. Corvid neophobia is curious, as they are also known to be highly innovative, yet neophobia is generally thought to limit innovation⁴² and characterize narrow ecological niches¹⁷. Within corvids, species and individuals differ in neophobic propensities^{13,43–45}, as well as socio-ecological factors, such as range (how geographically widespread a species is), sociality, caching (hiding food for later use) behaviour, and tool-use^{40,46–50}. It is currently unknown what drives this high neophobia in corvids, for instance, whether they follow the same pattern as parrots relating to diet type (e.g.¹⁰), or if there are different drivers of this variation. Corvids are therefore an optimal choice for these questions, however, to our knowledge, no study has yet compared neophobia comprehensively across many corvid species, with repeated testing for individual repeatability, and directly testing the influence of socio-ecological factors.

We conducted a multi-lab collaborative study on corvid neophobia with three main aims: 1. compare species, 2. investigate the effect of socio-ecological factors, and 3. assess individual temporal and contextual repeatability. For 10 corvid species (241 subjects: Figure 1), we tested behavioural responses - specifically latency to touch familiar food – in three conditions: novel objects, novel food, and control condition (familiar food alone), with each condition repeated 3 times over 6-8 weeks (3 test rounds, 1 trial per condition per round, every ~2 weeks). Individuals were tested while alone (all species except ‘Alalā, *Corvus hawaiiensis*) to control for social influences and enable repeated individual testing. Novel items were presented with familiar food to ensure responses were a result of the conflict between neophobia and desire for the familiar food, rather than, for example, exploration¹. Our response variable tested true food (and object) neophobia (i.e. fear of the appearance of the food), rather than dietary conservatism (i.e. latency to consume a novel food regularly in the diet)⁵¹. We use the terms ‘object neophobia’ and ‘food neophobia’ as we specifically tested trials in a foraging context/ near resources (i.e. familiar food) - recommended terminology outlined in⁵². We used a different colour/ flavour of novel food (jelly) in each round and only 20% of subjects touched the novel food, therefore latency to consume novel food was not an informative measure for within-

and between-species comparisons. We pooled resources across labs with the aim of increasing sample sizes and species representation. Tests were selected as not too time or labour intensive, given many labs were contributing data, whilst giving a meaningful cross-species comparison largely based on established methodologies (i.e. latency to eat/ approach familiar food in the presence of a novel item).

Firstly, we compared neophobia between corvid species. As neophobia levels can differ across novelty types⁵⁴, we examined the factors that could contribute to object and food neophobia separately. We predicted species differences would be present, with some species showing higher neophobic responses than other species, as indicated by previous comparative corvid research e.g.^{13,44}. Next, we tested for the influence of socio-ecological factors: range (mainland vs. island/endemic), use of urban habitats (urban habitat vs. only suburban/rural), hunting live animals (catch/kill/eat live birds/mammals vs. scavenging dead animals/ eggs/ insects/ non-meat only), adult sociality (territorial pairs vs family groups), maximum flock size (small <100 vs. large >100 individuals), food caching (specialised i.e. large amounts of a specific food during certain seasons vs moderate i.e. a variety of food across the year), and genus (*Corvus* or not) on neophobia. We selected two-level factors as we could reliably distinguish these categories for the tested corvid species from published research (Table 1). ‘Maximum’ flock size may not be representative of ‘typical’ flock size, and may be biased by study effort, however, this was the most suitable metric available for the species tested. We predicted that, like diet in parrots¹⁰, neophobia would relate closely to aspects of species ecology. Specifically, in line with previous research suggesting increased exposure to a wide variety of novel items leads to reduced neophobia (e.g. wide ranges or urban environments), we expected that species inhabiting a mainland range, or utilising urban habitats, would show lower neophobia compared to those that are island-endemics or using only sub-urban/rural areas^{12–14,17,18,55}. Lower neophobia was also expected from species living in larger flocks and family groups compared to small flocks and territorial pairs, due to the potential of risk-sharing between larger groups^{23,56}.

Dietary factors influence neophobia in other species¹⁰. The 10 corvid species tested were primarily generalists, though they differed in two factors relating to diet and foraging strategies: caching propensity and hunting of live animals. We therefore expected these factors may influence corvid

neophobia, though as they have not been previously tested in similar species, we had no a priori predictions for these factors. We included genus as a control for phylogenetic relatedness. Finally, we tested for individual temporal (i.e. same task at different time points - 3 test rounds) and contextual repeatability (i.e. different tasks measuring same cognitive ability - across control, novel food, novel object conditions; ⁵⁷). We predicted individuals would be largely repeatable across time and conditions, as there were only short delays between test rounds (~2 weeks), similar to a related study in 'Alalā (data included in our analysis)⁵⁸. Furthermore, a recent meta-analysis found repeatability to novel objects was larger in short-term than long-term studies ⁵².

Results

Species differences

Latency to touch familiar food differed across conditions (LMM: $X^2=316.05$, $df=2$, $p<0.001$), test rounds ($X^2=28.75$, $df=1$, $p<0.001$), and species ($X^2=93.03$, $df=9$, $p<0.001$). Subjects waited longer with a novel object or novel food present compared to the control condition (Tukey contrasts: novel object – control, $z=18.79$, $p<0.001$; novel food – control, $z=7.97$, $p<0.001$), and waited longer when a novel object was present than a novel food ($z=7.35$, $p<0.001$) (Figure 2A). Across all conditions, while latency to touch familiar food did not differ between rounds 1 and 2 (Tukey contrasts: $z=0.57$, $p=0.571$), it decreased in round 3 (rounds 1 – 3, $z=4.94$, $p<0.001$; rounds 2 – 3, $z=4.35$, $p<0.001$) (Figure 2B). Additionally, latency differed across species (Figure 3). 27 of 133 subjects touched the novel food (jelly) at least once (9 more than once): 2/18 carrion crows, 5/15 ravens, 2/24 Eurasian jays, 1/9 blue jay, 11/13 large-billed crows, 2/10 Clark's nutcrackers, 1/14 azure-winged magpie, 3/9 New Caledonian crows. A potential study confound is that most species were housed and tested at different labs. Therefore, lab is largely correlated with species. Three species were tested at two different labs - using exploratory analysis, we found that lab affected latency to touch familiar food in pinyon jays but not carrion crows or azure-winged magpies (Figure S1).

To aid in standardizing latencies across labs as well as control for baseline neophobia and current motivational state, we created pairwise difference scores by subtracting the control latencies from the novel object and novel food latencies for each round and individual. Positive difference scores represent slower approaches to familiar food when a novel item is present (i.e. neophobia) and negative difference scores represent faster approaches. The novel object difference scores differed across species (LMM: $X^2=47.02$, $df=9$, $p<0.001$) and round ($X^2=8.18$, $df=1$, $p=0.017$), with some species differences (Figure 4A; Table S1). Using novel object difference scores, common ravens were more neophobic than azure-winged magpies, large-billed crows, New Caledonian crows, Clark's nutcrackers, blue jays and pinyon jays; azure-winged magpies, pinyon jays and Eurasian jays were more neophobic than large-billed crows; Eurasian jays were more neophobic than blue jays and Clark's nutcrackers; carrion crows were more neophobic than Clark's nutcrackers and large-billed crows; 'Alalā were more neophobic than blue jays, large-billed crows, Clark's nutcrackers, New Caledonian crows, pinyon jays (Figure 4A).

The novel food difference scores also differed across species ($X^2=23.49$, $df=8$, $p=0.003$) but not round ($X^2=5.58$, $df=2$, $p=0.062$). Note that 'Alalā were not tested in the novel food condition and are removed from this analysis. Using novel food differences scores, Eurasian jays were more neophobic than all other species (Figure 4B; Table S2). Overall, for both object and food conditions, most species were neophobic with mean difference scores greater than 0, with only New Caledonian crows showing a negative mean difference score for the food condition.

Effect of socio-ecological factors

Using novel object difference scores, object neophobic responses were affected by urban habitat use ($X^2=8.23$, $df=1$, $p=0.007$), adult sociality ($X^2=11.59$, $df=1$, $p<0.001$), caching ($X^2=4.06$, $df=1$, $p=0.04$), and maximum flock size ($X^2=6.00$, $df=1$, $p=0.014$), but not range ($X^2=1.85$, $df=1$, $p=0.174$), live hunting ($X^2=3.68$, $df=1$, $p=0.55$), or genus ($X^2=1.42$, $df=1$, $p=0.233$). Specifically, species that use urban habitats (as well as other habitats), live in larger flocks and family groups, or are specialised

cachers were less neophobic than those that do not or have very limited use of urban habitats, live primarily in territorial pairs, in smaller flocks, or are moderate cachers (Figure 5A). Using novel food difference scores, food neophobia was only affected by maximum flock size ($X^2=8.99$, $df=1$, $p=0.003$) and not range ($X^2=2.72$, $df=1$, $p=0.100$), urban habitat ($X^2=0.33$, $df=1$, $p=0.564$), adult sociality ($X^2=1.98$, $df=1$, $p=0.160$), caching ($X^2=0.25$, $df=1$, $p=0.621$), live hunting ($X^2=0.10$, $df=1$, $p=0.756$), or genus ($X^2=3.51$, $df=1$, $p=0.061$). In contrast to the object neophobia finding, species that typically live in small flocks were less neophobic of novel food than those living in large flocks (Figure 5B).

Individual temporal and contextual repeatability

Across all species, individuals' responses to novel stimuli were temporally repeatable across test rounds (1-3) and contextually repeatable across conditions (control, novel object, novel food) (repeatability estimate: $N = 217$, $R = 0.462$, $p < 0.001$, $CI = 0.399-0.520$). In addition, responses were temporally repeatable within each condition (control: $N = 216$, $R = 0.542$, $p < 0.001$, $CI = 0.472-0.619$; novel object: $N = 215$, $R = 0.548$, $p < 0.001$, $CI = 0.467-0.628$; novel food: $N = 132$, $R = 0.477$, $p < 0.001$, $CI = 0.380-0.582$) (Table S3). Within-species analysis indicated all species were temporally repeatable, except for the New Caledonian crows (all conditions), azure-winged magpies (novel food only) and large-billed crows (novel object only), with contextual repeatability in all species except for the New Caledonian crows (Table S4). Note: 'Alalā were not tested in the novel food condition.

Discussion

In our multi-lab collaborative study, we tested responses (latency to touch familiar food) of 10 corvid species to novel objects and novel food (beside familiar food), compared with a control baseline condition (familiar food alone). We found: a) some species differences in latency to touch familiar food in the presence of a novel object or novel food relative to baseline, b) effects of four socio-ecological factors - urban habitat use, adult sociality, maximum flock size and caching - on object

neophobia, and an effect of maximum flock size on food neophobia, and c) individual temporal and contextual repeatability across species, as well as within species for all species except New Caledonian crows (all conditions), azure-winged magpie (novel food) and large-billed crow (novel object). The novel object and novel food conditions elicited higher neophobic responses (i.e. higher latencies) than the control condition, and the novel object higher neophobic responses than the novel food condition. This latter finding is potentially because the novel foods (3 jelly colours/ flavours) were more similar to one another than the novel objects (3 different objects). Additionally, neophobic responses reduced across rounds, with lower latencies in test round 3 than either round 1 or 2.

Using difference scores, we found that species differed in object and food neophobia, i.e. latency to touch familiar food in presence of novel item. We found that: common ravens, carrion crows, ‘Alalā and Eurasian jays were more object neophobic than most other species, with Eurasian jays being more food neophobic than all other species. Mean difference scores showed most species were highly avoidant of novel items (i.e. positive scores indicating neophobia), instead of demonstrating attraction (i.e. negative scores). Only 20% of subjects touched the novel food, indicating subjects may not have perceived the jelly as food but rather as an object. We selected the same measure (latency to touch familiar food) for all conditions and treated the ‘novel food’ comparably to the novel object condition.

The critical test for interpreting these species differences - not possible in most previous studies with single or small numbers of species/ individuals - was to test for influences of socio-ecological factors that naturally differ between these corvid species. We found that four factors influenced object neophobia: urban habitat use, adult sociality, maximum flock size and caching, while range, hunting live animals and genus did not. Specifically, object neophobia was lower in species using urban habitats (n=5 species), living in family groups (n=3), large flocks (n=6) and specialised cachers (n=4 species) compared with those only using suburban/ rural areas (n=5 species), living primarily in territorial pairs (n=7), in small flocks (n=4), or moderate cachers (n=6). Only flock size influenced food neophobia, with those living in small flocks showing lower neophobia than those in large flocks. Different socio-ecological predictors emerged between conditions suggesting the novel foods were

not perceived simply as novel objects. Alternatively, the strength of neophobic responses were dependent on object features.

We expected urban habitat use to influence neophobia based on previous research with other species, such as within-species comparisons in common myna¹² and black-capped chickadees⁵⁵. Urban habitats are typically rich in novel stimuli, including human-made litter and structures. Consequently, individuals and species inhabiting these areas are frequently exposed to a variety of novel objects and may become habituated to such novelty, or face selective pressures that favour less neophobic individuals, although the evidence for either process is mixed⁵⁹. Additionally, there are two ecological explanations for why reduced neophobia could be beneficial in cities. The costs of neophobia may outweigh the benefits in urban habitats: human objects may become useful resources (litter as food or an effective tool), an opportunity lost by a high neophobic response (i.e. Neophobia Threshold Hypothesis). Alternatively, urban environments may have a lower predation risk, thus limiting dangers associated with novel object exploration^{14,17} (i.e. Dangerous Niche Hypothesis), although the true predation risk experienced is still unclear.

Similarly, we expected adult sociality to influence neophobia, with lower object neophobia in large flocks or family groups due to increased risk-sharing, compared with species living primarily as territorial pairs while adult or small flocks²³. Social presence has been shown in some species, including corvids, to have a facilitating or inhibiting effect on neophobia and exploration^{31,56}. We differentiated species as ‘territorial’ vs ‘family groups’ according to the most prevalent social organisation⁴⁶. Some species do have flexible systems based on fission-fusion, such as the common raven⁶⁰, thereby, they may be territorial as adults/ during breeding season but fairly tolerant of one another as juveniles or outside of breeding season⁶¹. We therefore included a second sociality related factor: ‘small’ (<100 individuals) vs. ‘large’ maximum flock size (>100 individuals).

There was an effect of caching, which may relate to differences between moderate and specialised cachers in the amount and type of food items that they cache. Our caching differentiation was based on food caching⁶² (Table 1), though some corvids also cache objects^{62,63}. There was insufficient data available to differentiate all species according to object caching variation, though this may be possible in future as data becomes available. We did not find an effect of hunting live animals on neophobia

(hunting live animals n=6 species vs not n = 4) - our main dietary related measure, as these corvids have largely similar diets. Different types of novel food, such as animal carcasses, may illicit an effect.

We found no effect of range (mainland n=8 vs island n=2 species) on neophobia, contrasting with previous results from parrots¹⁰, as well as the “island tameness theory”, suggesting that island populations may be less neophobic because they have evolved with fewer environmental dangers⁶⁴. Only the New Caledonian crows and ‘Alalā were island-endemics, therefore interpretation of this finding should be tentative, particularly as the New Caledonian crows were wild-living. Finally, we found no effect of genus (Corvus n=5 or not n=5 species) on neophobia. Further phylogenetic controls should be possible in future if additional reliable phylogenetic data for corvids become available, and species sample increased above 20 species^{65,66}.

All species, other than New Caledonian crows (all conditions), azure-winged magpies (novel food) and large-billed crows (novel object), showed individual repeatability over time (i.e. 3 test rounds over 6-8 weeks). Similarly, all species, except for New Caledonian crows, showed individual repeatability across all 3 conditions. The New Caledonian crows were the only wild-living birds (temporarily captive) of the sample, which may have influenced their responses. It may also be related to habituation to the captive situation (i.e. habituating over the 3 test rounds, variably influencing their responses to novel items). Individual flexibility (i.e. lack of repeatability or inconsistency) may be adaptive in the wild, where conditions can vary more widely than captivity. Additionally, individual inconsistency has been found in other corvid species, including pinyon jays and Clark’s nutcrackers exploratory responses to novel environments and objects (no familiar food present)³². Some of these same individuals were tested in the present study, highlighting neophobia may vary within/between individuals depending on neophobia types, or study design aspects, like task type. It may also vary depending on the subject source as this group of pinyon jays and Clark’s nutcrackers were originally sourced in the wild, though lived in captivity - further testing within-species comparing captive to wild-caught individuals would be necessary to test this further.

The main study limitations, also applicable to many previous comparative cognition studies, were some unavoidable lab differences and prior history differences (Table S5; ⁶⁷). For example, although

most species (11/13 groups) were not tested in previous neophobia-focussed experiments, many have been exposed to varying levels of novelty (e.g. food, objects, humans, predators) in experimental contexts, enrichment and training. Similarly, three labs had a controlled food schedule (per standard lab protocols), though it is possible that food caches were available. We aimed to test all available subjects, however, as 5 labs used voluntary participation, this may have influenced overall subject availability. We primarily used difference scores (novel condition minus control data) to aid in standardising latency scores across labs and control for baseline neophobia ¹. This method has the important advantage of controlling for differences in activity rates, which could lead more active individuals/ species to contact familiar food faster, which is usually not controlled for in object exploration tests, thus is a strength of the classic Greenberg neophobia test ¹. We differentiated each socio-ecological factor tested on 2-levels using published data (e.g. ^{46,62}). Some factors could be explored on further levels (e.g. scale or distribution size for range) if additional supporting evidence becomes available for each species. We counterbalanced testing order across subjects and species; however, it is possible that this may artificially inflate repeatability or species differences by creating among-individual/ species differences in carry-over effects. Future research could take a standardisation approach or test this effect systematically within species.

There were differences in species sample sizes, indicating care should be taken with any generalisations beyond samples to wider species-levels. Our samples were also primarily captive individuals (only New Caledonian crows were wild-living prior to testing, though 4 other species were originally wild-born prior to long-term captive holding, Table S5), which may influence neophobia ⁵. For example, a meta-review found lower levels of baseline neophobia among wild-caught individuals, as they may experience more variation in an ecological setting ⁵. Population differences can be driven by plasticity (resulting in individual-level habituation) and/or selection processes (resulting in changes in population-level neophobia over generations) - future work may aim to tease apart these aspects.

This study was a necessary first step into establishing a multi-lab collaboration, and captive birds allowed us to identify individuals, conduct repeated testing and control the environment, which could be expanded upon in future, for instance, to include corvids in the field ¹³. The novel object paradigm,

as in Mettke-Hofmann et al.'s (2001) parrot study¹⁰, allows for future comparison beyond corvids and parrots. Testing more widely within groups of the same species from different backgrounds, as well as between species, and expanding these types of collaborative approaches to test other bird groups to explore the drivers of neophobia in birds more generally, is a recommended focus and planned for future research by the ManyBirds Project⁸⁰. Comparing captive to wild-caught individuals would enable further exploration of whether species differences in neophobia are robust to developmental context, suggesting these are evolved differences. Furthermore, this large data set could be expanded upon to explore factors like age (e.g. testing juveniles per species) and social context influence (e.g. testing with a conspecific present). Additionally, other aspects of neophobia, such as novel environments, predators or humans (e.g.⁴⁴) could be tested, as well as different food types (e.g. coloured seed), or closer exploration of novel item interactions.

There are several wider study implications. When comparing neophobia in different species, it is important, where possible, to consider the role of socio-ecological factors, like diet, habitat use and sociality. Neophobia can influence how an animal interacts with novel problems, so should be tested as a baseline, particularly in new species/individuals, when conducting cognition research. The world is fast becoming more urbanised due to human activity, with many species being forced to adapt to changing environments or risk survival⁷. As neophobia may impact how quickly a species or individual can adapt, it is a useful tool in designing conservation applications, such as in reintroductions^{38,54,58}. For example, the presentation of new bird feeders or safe nesting sites could be modified according to the species/ individual's level of neophobia, and more neophobic individuals may require more pre-release training than others. Additionally, for species that are extinct in the wild, comparative behavioural/ cognitive data from related species with similar flock sizes, group sociality, or habitat types may determine the extent that long-term conservation breeding erodes natural responses. Therefore, neophobia and related research provides valuable information in basic and applied research.

In conclusion, we established a global collaborative network among corvid researchers to investigate the socio-ecological correlates of corvid neophobia. Neophobia can impact cognitive performance^{36,54}, but is often not tested or accounted for in comparative research – this study

contributes to resolving this issue. For example, when comparing species cognitive performance, one needs to show species don't differ in neophobia, or else it needs to be controlled for statistically. Furthermore, individuals should be habituated until new experimental items elicit a latency similar to baseline feeding latency – although often done, studies often do not report the effectiveness of the habituation procedure. It contributes to a growing push to conduct multi-species comparisons while simultaneously facilitating other collaborative future work between these labs. Though species differences in neophobia are well-known among those working with corvids, they are typically incorporated into study designs (like a habituation phase to new stimuli) than studied in their own right or comparatively. By investigating neophobia across related species that vary in socio-ecological factors and feature frequently in behaviour/ cognition studies, this study has broad implications for those interested in behavioural ecology, comparative psychology and other related fields.

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Author contributions

R.M., M.L.L., A.F. A.L.G. and N.S.C. conceived the study idea and research design. R.M. and M.L.L. project managed the study. R.M., S.A.R. and J.R.S. analysed the data, R.M., M.L.L. and J.R.S. produced the figures. R.M., A.F., K.F.B., E.G.P., K.G., L.B.L., A.L.G., Y.L., M.S., A.K., P.S., L.W., L.M.W., Y.Z. collected the data. R.M., A.F., I.C., E.G.P., A.L.G., L.B.L. coded the videos. R.M. and I.C. wrote the manuscript, with comments and feedback from all other authors. R.M., K.B., T.B., K.G., E.I., D.M.K., Z.L., A.N., J.R.S., A.H.T., N.S.C. provided funding to support the study.

Declaration of interests

The authors declare no competing interests.

Main-text Figure and Table Legends

Figure 1. Phylogenetic tree. Sourced from ⁵³ (www.timetree.org, July 2021) with sample size (n=x) and relative object neophobia score per species (mean latency to touch familiar food difference score i.e. novel object minus control value) - higher score indicates higher neophobic response to novel object. * denotes species tested at 2 labs.

Figure 2. Latency to touch familiar food across all species. (A) across conditions: control (N=216), novel food (N=132, 'Alalā were not tested for novel food neophobia), and novel object (N=215) conditions all differed from each other. **(B)** Across test rounds: round 3 differed from round 1 and 2, while round 1 and 2 do not differ from each other. Raw data; individual points represent subject means over rounds; lines represent median. *** $p < 0.001$

Figure 3. Latency to touch familiar food in each condition for each species. Some species differed in mean latency. Individual points represent subject means over rounds, points with error bars represent species means and 95% confidence intervals.

Figure 4. Species comparison using difference scores. Mean latency difference scores varied across species for **(A)** novel object neophobia and **(B)** novel food neophobia i.e. latency to touch familiar food in presence of novel item, related to Table S1 and Table S2. Positive difference scores represent slower approaches to familiar food when a novel item is present (i.e. neophobia) and negative difference scores represent faster approaches. Points represent individuals.

Figure 5. Effect of socio-ecological factors on neophobia. Linear mixed model on socio-ecological factors affecting latency to touch familiar food, using difference scores showed effects of urban habitat, adult sociality, caching and maximum flock size on novel object neophobia **(A)** and effect of maximum flock size on novel food neophobia **(B)**. Positive difference scores represent slower approaches to familiar food when a novel object is present (i.e. neophobia) and negative difference scores represent faster approaches. Points represent individual subjects and horizontal bars represent medians.

Figure 6. Example of novel objects. Objects A, B and C. Eurasian jays, Clayton Lab

Table 1. Socio-ecological factors of corvid species tested. Differentiation within factors restricted to 2 levels reflecting availability of published data to support these distinctions across all species. * Typically applicable for Europe (where the common ravens tested in this study were held and sourced); ravens have used/use cities at some North American sites (personal observation). ** One carrion crow population in Spain have helpers at the nest (i.e. cooperative breeding), though this is not reported in other populations⁷¹

506 **STAR Methods**

507

508 **Resource Availability**

509 **Lead contact**

510 Further information and requests for resources should be directed to and will be fulfilled by the lead
511 contact, Rachael Miller (rmam3@cam.ac.uk).

512

513 **Materials availability**

514 The study did not generate new unique reagents.

515

516 **Data and code availability**

517 The data have been deposited at Figshare (<https://figshare.com/s/16a77c3ab4e7569f0d98>) and are
518 publicly available as of the date of publication. Accession number is listed in the key resources. The
519 original code has been deposited at Figshare (<https://figshare.com/s/16a77c3ab4e7569f0d98>) and are
520 publicly available as of the date of publication. DOI number (10.6084/m9.figshare.14806704) is listed
521 in the key resources. Any additional information required to reanalyse the data reported in this paper
522 is available from the lead contact upon request.

523

524 **Experimental Model and Subject Details**

525 We tested 241 corvid subjects (141 males, 95 females, 5 unsexed, primarily adult birds - 5/9 New
526 Caledonian crows & 25/108 ‘Alala were juveniles) across 10 species and 10 lab teams worldwide
527 (Table S5). The sample sizes ranged from 9 to 108 subjects per species (mean = 24; median = 15),
528 depending on subject availability. All subjects could be identified individually (e.g. by coloured leg
529 rings). Species tested were common ravens (n=15), carrion crows and carrion/hooded hybrid crows
530 (n=18), large-billed crows (n=13), New Caledonian crows (n=9), ‘Alalā (n=108), Eurasian jays

(n=24), pinyon jays (n=21), blue jays (n=9), Clark's nutcrackers (n=10) and azure-winged magpies (n=14). Each lab housed and tested their own species according to the ethical and housing conditions required within each country, with two labs holding more than 1 species, and 3 species each tested at two different labs (Table S5). Additional subject information, including age (adult or juvenile) and test cage size, is provided in Table S5. Individual labs were responsible for the data collection of their birds but were provided with the same protocols to ensure the methodology remained consistent and were in regular contact with the organising team.

These species differ in several specific socio-ecological factors: range, urban habitat use, hunting live animals, food caching, adult sociality and maximum flock size (Table 1). Range was classed as mainland vs. island endemic ⁶⁸, urban habitat as use of urban vs. only rural/ suburban habitats ^{68,69}, hunting live animals (i.e. catch/ kill/ eat birds/ mammals) vs. not (i.e. only scavenging dead animals/ eggs/ insects/ non-meat) ^{68,69}, sociality while adult as living primarily in territorial pairs (throughout the year or seasonally) vs. within family groups (e.g. dominant breeding pair with offspring) ⁴⁶, maximum flock size as small (up to 100 individuals) or large (over 100 individuals) ^{69,70}, caching (hiding food for later use) as specialised (i.e. large amounts of a specific food during certain seasons) vs moderate (i.e. a variety of food across the year) ⁶², and if they were from the *Corvus* genus or not ⁶⁸.

Apparatus/materials

There were three conditions: control (familiar food alone), novel food, and novel object (novel items beside familiar food). The familiar food (placed in a familiar food bowl) varied between bird groups, depending on the regular diet in each lab. The novel food consisted of jelly (no added sugar/ sweeteners) in 3cm³ blocks, selected as an edible, safe food type that is novel to all tested species and not a part of any one species regular diet, also placed in a (different) familiar food bowl. There were three colours/flavours of jelly used: orange, purple/blackcurrant, and green/lemon & lime, which were presented individually across the three rounds. As the species typically have different diets, and the food needed to be equally novel for them all, a colourful, human-made food such as jelly provided an

ideal option (with prior ethical approval including from a Home Office appointed Named Veterinary Surgeon, Cambridge University). The novel objects came in three variations, but all had the same properties: they were made of multiple items and textures, with no part that could look like eyes (to avoid resembling predators), and all contained the colours blue, yellow, green, and red⁵⁸. Part of the objects also had to be shiny (note. the popular belief that shiny objects are attractive to corvids has been debunked⁷²), and the objects were all between one third and one half the size of the subject (so the size of the object itself varied with species; Figure 6). All birds were tested in a feeding or testing compartment/cage, which varied in dimensions by lab, but gave the birds as much room as possible to avoid and/or approach stimuli. The testing area was familiar to the bird, or else the bird was habituated to the cage prior to testing.

Procedure

The tests involved measuring behavioural responses to novel food and novel objects beside familiar food, in relation to baseline measures of familiar food only (control). As so few individuals touched the novel food during trials (20% subjects), this metric was not informative for explaining variation within or between species. Data collection took place outside of breeding season, with captive individuals, other than the New Caledonian crows, which were wild birds temporarily held in captivity. For most species/groups, individuals were temporarily separated in visually isolated testing compartments, though typically not acoustically isolated i.e. could hear groupmates ('Alalā were left in their regularly housed social groups for tests to reduce stress, which were primarily 2-bird breeding pairs). Separation was achieved via voluntary participation in 5 labs (Eurasian jays, New Caledonian crows, common ravens, 'Alalā, T.B. lab carrion crows and T.B. & J.J.M.M. lab azure-winged magpies), whereas in the 5 other labs, the birds were physically moved by an experimenter to the familiar testing area as per the typical testing procedures in each lab. The novel item (food or object) was placed beside the familiar food dish (20cm for larger species i.e. *Corvus* genus, 10cm for smaller species i.e. other species), with items placed in the same location (e.g. a table/ platform/ mesh wall – large enough so that the bird could approach slowly from more than a body length away) for all tests

and individuals within each species. Where possible, the stimuli were present before the subject entered the testing compartment (all species except ravens). The test trial started when the subject entered the testing compartment (or experimenter left compartment). Each trial lasted a maximum of 10 minutes (600 seconds) or ended when the subject touched the familiar food (i.e. beak contacted food).

Each novel test ‘round’ was conducted 3 times with 1 trial per condition per round (i.e. 9 trials in total) to allow for testing for individual repeatability within and between conditions. The control trial was conducted within 48 hours of both novel tests (min = 24 hours, max = 48 hours), and all in the morning. We note that three labs had a controlled food schedule (Table S5), however the food schedule within lab and individual was consistent between the control and experimental conditions, therefore we can assume motivation was similar. Each round of testing (1 trial each of food- control-object conditions) took place with approx. 2 weeks between each round i.e. week 1: food-control-object, week 3: food-control-object, week 5: food-control-object. Therefore, testing took approximately 6 weeks in total to complete per species/group. The order of presentation of the novel food and objects was counterbalanced across subjects and species, e.g. subject 1, round 1 – novel food type 1 (orange jelly), round 2 – type 2 (green jelly), round 3 – type 3 (purple jelly); subject 2, round 1 – type 3, round 2 – type 1, round 3 – type 2 etc. The object types and jelly colours were also counterbalanced across subjects and species. The testing schedule for half of the subjects was food-control-object in every round, and for the other half object-control-food in every round per group. All species were tested in all three conditions, except for the ‘Alalā, which were tested in the familiar food and novel object conditions only ⁵⁸ (due to Covid-19 pandemic limiting access for testing the novel food condition). Most individuals participated in all trials, with minimal missing data.

Our main measure was latency to touch familiar food signifying how long the individual took to touch a familiar, desirable food in the presence of a novel item. Any avoidance of the novel item (and thus familiar food) can then be interpreted as neophobia ¹. Latency to touch familiar food was used (rather than latency to eat) to control for any potential doubt as to whether the bird swallowed the food.

Statistical Analysis

Trials were recorded and all new videos (>1200 videos were newly collected; >650 ‘Alalā videos were coded previously for ⁵⁸ study) were coded in Solomon Coder ⁷³. 12-15% of video trials for each species/group were coded by a second coder to ensure inter-rater reliability: ‘Alalā: intra-class correlation coefficient (ICC) = 0.956, CI = 0.94-0.97, $p < 0.001$; all other species: ICC = 0.879, CI = 0.804-0.925, $p < 0.001$). Our main coder was unfamiliar with all study species and not aware of the hypotheses prior to coding.

We had three main research questions and associated analyses: 1. species comparison (main effects of species, condition and round, random effect of individual) 2. effect of socio-ecological factors (main effects of range, urban habitat, adult sociality, maximum flock size, caching, live hunting, genus) 3. individual temporal (main effect of round) and contextual (main effect of condition) repeatability of neophobia. The main dependent variable was latency to touch familiar food (0-600 seconds). Only 20% of subjects touched the novel food (jelly), therefore latency to touch novel food was not an informative measure. We used R (version 4.1.1) for all analysis. For Q1: we conducted a Linear Mixed Model (LMM) to assess which factors influenced latency to touch familiar food. The residuals of a LMM visually approached normal distribution (although the Shapiro-Wilk test indicated the distribution was different from normal, $W=0.9919$, $p<0.001$). We compared the LMM (packages `lm4`, `car`, functions `lmer()`, `anova()`, and `Anova()`) with the raw latency scores with an LMM using a log (base 10) transformation of latency + 1 (to avoid 0s). A likelihood ratio test (using `anova()` function) showed that the log-transformed model was preferred over the raw latencies (AIC raw = 21934.6, AIC log10 = 2761.5). Further transformations and Generalized Linear Mixed Models with other error distributions (poisson, gamma) and link (log) functions did not improve model fit. We therefore used the log-transformed latencies for all analysis, though we plot the raw latencies for visual clarity. With all LMMs, we used likelihood ratio tests to investigate the effect of the individual predictors (using `drop1()` function with best-fit model as input and setting test statistic to chi-square). We used Tukey comparisons (package `multcomp`, function `glht()`) for post-hoc tests without direct p-

value correction. P-value corrections, such as Bonferroni, limit the number of possible comparisons⁷⁴ and comparison of multiple species was a primary aim in this study.

In LMM 1, using all data, we included the main effects of condition, species, and round in the full model, with individual as a random effect and all variables set as factors. We initially included individual nested in lab (1-10 labs) as a random effect, but model selection showed no difference in fit from a model that did not include lab, so we opted for a more parsimonious model without lab for all models. A potential confound of our study is that most species were housed and tested in differing locations and conditions, including testing compartment size. Lab is therefore correlated closely with species. However, three species were tested at two locations; therefore, we checked these three species individually for an effect of lab (LMM, lab as main effects, individual as random effect; Figure S1).

To directly examine potential neophobia effects of novel objects and food, we calculated differences scores by subtracting the log-transformed latency values of the control condition from those of the novel object condition and separately for the novel food condition¹. Therefore, the control serves as the baseline for how long it usually takes an individual to touch familiar food (without novel items present). By subtracting this control value from the latency to touch familiar food when a novel object was present should help to standardize for any lab differences like cage size, e.g. species A has a small test cage so may have a shorter control latency due to this (less space to cover/ more likely to be closer at the start of the test) compared with species B with a large test cage. We created pairwise individual difference scores for each round and individual (e.g. individual 1, novel object round 1 minus control round 1; novel object round 2 minus control round 2). In LMM 2 (object difference scores) and LMM 3 (food difference scores), we included the main effects of species and round, with individual as the random effect.

For Q2: we conducted LMM 4 (object difference score) and LMM 5 (food difference score), with the main effects of range, urban habitat, adult sociality, maximum flock size, caching, live hunting, and genus, with individual as a random effect. The full models (including all predictor variables) had the best fit according to AIC. Though accounting for phylogenetic relationships can be important in some situations, testing for phylogenetic signal with fewer than 20 species is problematic^{65,66}, testing

is not advisable for all research questions (e.g. Q1)⁷⁵, and the corvid evolutionary tree is not yet well established for all tested species (e.g. conflicting genetic results about the closest relative for ‘Alalā’⁷⁶. Therefore, we did not include a phylogenetic control in our analyses. We did, however, include the variable ‘genus’ (Corvus or not) in our Q2 models. Additionally, we provide a phylogenetic tree for visualisation purposes with relative neophobia scores per species (Figure 1). In reporting all results, we avoid using the term ‘significant’⁷⁷. As 30 of 241 subjects were juveniles, we also re-analysed the data using only adult subjects, and our results still hold (i.e. statistical significance > 0.05 is the same for all models).

For Q3, we tested across species and within species for individual repeatability over time (across rounds) and over context (across conditions) using repeatability (R)⁷⁸. We extracted R estimates from linear models with individual as a random effect and bootstrapped 1,000 samples to generate 95% confidence intervals around the estimates (R package rpt, using rpt() function). For contextual repeatability, we included condition in the linear model, and for temporal repeatability, we included round in the model (Table S3 and Table S4). We used raw data rather than difference scores as the focus was on individual-level behaviour, where any unavoidable lab differences are constant, rather than between species (where it is important to use difference scores), as per several similar studies^{58,79} - difference scores would compound the error inherent to each measurement. Furthermore, as the non-object condition and the object (or food) conditions aim to capture different motivations, by subtracting them, we would lose the meaning behind each one.

The ‘Alalā control and novel object data was collected in a previous study⁵⁸. We used a comparable methodology while collecting the new data with 9 corvid species for the present study. We edited the ‘Alalā data set by introducing a maximum cut-off of 10 minutes per trial (original dataset 60 minute trials) – any individuals that did not touch familiar food within 10 minutes were assigned 600 seconds – to ensure comparability.

Example video trials can be found at: <https://youtu.be/Lhzyk3srmdg>.

694 **Ethics Statement**

695 For animal research, all applicable international, national and/or institutional guidelines for the care
696 and use of animals were followed. For N.S.C's Comparative Cognition lab, this non-invasive
697 behavioural study with birds was conducted adhering to UK laws and regulations and was covered
698 under a non-regulated procedure through University of Cambridge, approved by the Home Office
699 appointed Named Animal Care and Welfare Officer, Named Veterinary Surgeon and Chairperson for
700 the Psychology and Zoology Department Animal User's Management Committee. For D.M.K lab,
701 research protocol approved by University of Manitoba's Animal User Committee (F18-041) and
702 complied with the guidelines set by the Canadian Council on Animal Care. For A.N., experiments
703 were approved by the national authorities (Regierungspräsidium). For E.I. lab, the experimental
704 protocol (number 9069) authorised by the Animal Care and Use Committee of Keio University, for
705 capturing wild crows (numbers 27924005 and 29030001) authorised by the Japanese Ministry of the
706 Environment. For J.R.S. lab, research protocol approved by University of Nebraska-Lincoln IACUC
707 (number 1708). For A.G. contribution, work was approved by San Diego Zoo Global's animal care
708 and use committee IACUC (number 16-009) and conducted under USFWS Permit (number TE-
709 060179-5) and State of Hawaii Division of Forestry and Wildlife permit (number WL16-04). For K.G.
710 lab, a research protocol approved by Luther College IACUC (no. 2019-4). For A.H.T. lab, a
711 University of Auckland Animal Ethics Committee (no. 001823). For T.B. lab, work on foraging
712 decisions, including this non-invasive behavioural study, was conducted adhering to Austrian law (2.
713 Federal Law Gazette no. 501/1989) and approved by an Animal Ethics and Experimentation Board of
714 the Faculty of Life Sciences, University of Vienna. For Z.L. lab, the study was conducted according to
715 the Ethics Review Committee of Nanjing University (no. 2009-116), under Chinese law, no specific
716 approval was required for this non-invasive study.

717

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