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# Exploration of A novel environment is not correlated with object neophobia in wild-caught house sparrows (*Passer domesticus*)



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## ARTICLE INFO

#### ABSTRACT

Keywords: Behavioral syndrome, Correlations Neophobia Passer domesticus Novel object, food, and environment trials have been widely used to understand how individual variation in neophobia (an aversion to novelty) relates to variation in endocrine, physiological, and ecological traits. However, what is often missing from these studies is an evaluation of whether an animal's response to one type of neophobia test is reflective of its response to other neophobia tests. In this study we investigated whether spatial neophobia was significantly correlated with responses to a novel object paradigm. In spatial neophobia trials, wild-caught house sparrows (n = 23) were allowed access to a novel environment (an adjacent cage with familiar objects placed in new locations). Time to first enter and total time spent in the novel environment were assessed. In novel object trials, birds were exposed to a new novel object in, on, or near their food dish and time to approach and feed from the dish was measured. Results indicate that neither time spent in a novel environment nor time to first enter a novel environment were correlated with an individual's average response to novel object trials. Therefore, these two tests may be assessing two discrete behaviors that involve separate decision-making processes and functional circuits in the brain.

#### 1. Introduction

Neophobia, an aversive response to novelty, is a behavior that directly influences the ability of animals to inhabit new environments, use novel resources, and avoid harmful situations (Greenberg and Mettke-hofmann, 2001). As novel urban and suburban environments replace natural environments worldwide, it becomes increasingly important for researchers to understand neophobia in wild populations (Crane et al., 2020; Greggor et al., 2016; Mazza et al., 2021). Neophobia is most commonly measured as an animal's reluctance to approach a novel object (Fischer et al., 2016; Stöwe et al., 2006), consume a novel food (Forss et al., 2019; Sol et al., 2011), or explore a novel environment (Kozlovsky et al., 2014; Verbeek et al., 1994). Many researchers evaluate neophobia in only one of these novel contexts, assuming that an animal's response to one type of novel stimulus is consistent with another (e.g., food neophobia vs object neophobia). However, in studies that have examined responses to multiple types of novelty in the same individuals, some studies have found positive correlations between individual novel object and food responses (Kimball et al., 2022) and negative correlations between novel object and environment responses (Cole and Quinn, 2014; Verbeek et al., 1994), whereas others have found inconsistent results in individual responses to novel objects, food, and environments (Damas-Moreira et al., 2019; Fox et al., 2009; Szabo and Ringler, 2022). Uncorrelated results from different types of neophobia tests (i.e., a lack of convergent validity) suggests that different tests may not be measuring the same trait (Campbell and Fiske, 1959). This can lead to jingle fallacies, where a single trait label ("neophobia") actually describes two functionally different traits measured with different tests (perhaps, "feeding neophobia" vs. "spatial neophobia") (Carter et al., 2013). Our goal in this study was to determine if neophobia was correlated across object and spatial contexts in wild-caught house sparrows (*Passer domesticus*).

House sparrows show wide and repeatable individual variation in novel object and novel food responses, with some individuals displaying extremely high neophobia and others appearing indifferent towards novelty (Ensminger and Westneat, 2012; Kelly et al., 2020; Kimball et al., 2022; Liebl and Martin, 2014; Martin and Fitzgerald, 2005). This wide individual variation makes house sparrows ideal to examine possible intra-individual correlations among different types of neophobia tests. Previous research has shown positive correlations between individual object and food neophobia responses in house sparrows (Bókony et al., 2012; Kimball et al., 2022). However, to our knowledge,

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Fig. 1. Experimental design for A) novel environment and B) novel object paradigms used to assess house sparrow neophobia. Novel right or left cage treatments or 2 control days were randomized over 4 days, and 3 novel object and 2 control days were randomized over 5 days. Trials lasted 1 h, after which the bird was returned to its home cage (if necessary) and the divider closed, or the objects were removed and the normal food dish was present for the remainder of the day. Objects ranged in size from smallest (pink puffs):  $3 \text{ cm} \times 3 \text{ cm}$  to largest (red dish):  $10 \text{ cm} \times 10 \text{ cm} \times 4 \text{ cm}$ .

no studies have correlated object and spatial neophobia responses in house sparrows, despite existing studies measuring both traits (Ben Cohen and Dor, 2018; Quesada et al., 2022). If spatial and object neophobia paradigms are measuring the same underlying trait, we would expect an individual's latency to enter a new environment and total time spent in a new environment to be significantly correlated with its latency to approach and feed in the presence of a novel object. If they are measuring different traits, we would expect these responses to be uncorrelated. While our a priori goal was to measure "spatial neophobia," it is important to note that an animal's latency to enter and spend time in an unfamiliar environment could also be interpreted as exploratory behavior (which could be distinct from neophobia) or neophilia (a preference for or attraction to novelty). However, many neophobia paradigms consider exploration of a novel environment a measure of neophobia (e.g., Mazza et al., 2021), and neophobia is often explicitly defined to include a spatial component, e.g., as "avoiding novel predators, foods, objects and locations" in Greggor et al. (2015). Evidence suggests that neophobia and neophilia are independent traits (Greenberg, 2003; Greenberg and Mettke-hofmann, 2001; Mettke-Hofmann et al., 2009), although both influence an individual's response to novelty. Therefore, even if we assessed individual-level correlations between object neophobia and spatial neophilia (rather than between object and spatial neophobia), understanding how individual responses to novelty change in different contexts is still a topic worthy of examination.

# 2. Methods

### 2.1. Study subjects

Adult house sparrows (n = 8 females, n = 15 males) were captured using mist nets at bird feeders in several different locations in East Baton Rouge Parish from April through July 2021, and in December 2022. Because the presence of conspecifics can affect neophobia in house sparrows (Kelly et al., 2020), sparrows were singly housed in cages (56 cm length x 45 cm width x 33 cm height, with solid metal cage dividers separating them from identical adjacent cages on the left and/or right) in a vivarium at Louisiana State University with unlimited access to mixed seeds, grit, a vitamin-rich food supplement (Mazuri small songbird diet), and water. Sparrows were maintained at natural day length (13 L:11D) for three weeks to acclimate to the captive environment before trials began. Animals were collected under a Louisiana State Scientific Collecting Permit and all experimental procedures approved by the Louisiana State University Institutional Animal Care and Use Committee under protocol 21–010. We used approved methods for bird capture, transport, and husbandry as specified in the Ornithological Council's Guidelines to the Use of Wild Birds in Research (Fair et al., 2010). After this behavior-only study was complete, birds were used for another research project, so they were not euthanized.

#### 2.2. Spatial and object neophobia trials

Sparrows were visually (but not acoustically) isolated from neighbors during behavioral trials. Three days before trials began, all birds were moved to the center cage of a cage rack where the center cage was separated from empty cages on the left and right by opaque dividers. Center cages had food and water dishes, a sand bath for dustbathing, and three different perch types: plastic, manzanita branch, and flexible latex. In the novel left and right cages, familiar objects were rearranged so that the perches and dust bath were in different locations than the center cage and each other, and food and water dishes were removed to keep this test independent of food motivation (see Fig. 1A). This design kept the environment – but not the objects within the environment – novel, to prevent conflating novel object and novel environment responses. Object and spatial neophobia trials took place on separate weeks. During object neophobia weeks, sparrows experienced five trials over five consecutive days, with each sparrow randomly receiving three of seven possible objects and two days of control (no object) trials, in a random order. The remaining four objects were used in a separate study, so that all individuals were eventually exposed to all seven objects. During spatial neophobia weeks, sparrows experienced four trials over four days, with each sparrow randomly undergoing a control (no divider opening) or experimental (right or left cage) trial. The first group of sparrows (n = 1 female, n = 5 males) was tested for object neophobia before spatial neophobia, and the second and third group of sparrows (n = 7 females, n = 10 males) underwent novel object testing after spatial neophobia trials (14.3  $\pm$  8.3 days between spatial and object trials).

For spatial trials, researchers entered the room 30 min after lights on, began video recordings, and opened either the left or right cage divider 5 cm or wiggled the divider as a control, and then left the room. We recorded 1 h of behavior using an array of pole-mounted cameras (ZOSI Z18.5.T.2) connected to a DVR (ANNKE Model DM310) to measure latency to enter the new environment and duration spent exploring the new environment. At the end of the 1 h trial, we stopped the video recording, moved birds back to the center cage if necessary, and closed dividers. Videos were only observed during the 1 h period when researchers were not in the room. All sparrows were given access to both the left and right cages on different days, in a random order.

Object trials were completed as previously described (Kimball et al., 2022). Briefly, sparrows were fasted overnight, and researchers entered the room 30 min after lights on, began video recordings, replaced the food dish with its treatment, and left the room. Novel objects were placed in, on, around, or directly over the food dish (see Fig. 1B); for controls, normal food dishes were replaced. We recorded 1 h of behavior as described for spatial neophobia trials. Objects were randomly selected, and the order of different object and control trials was randomly determined for each sparrow. Novel objects shared few common features (e.g., red color) that might target ecologically-relevant cognitive biases (Greggor et al., 2015), and have all been shown to significantly increase average latency to feed in house sparrows (Kelly

#### Table 1

Ethogram used for assessing house sparrow behaviors in BORIS. Point-type behaviors were discrete behaviors with no duration and state-type behaviors were behaviors with duration.

| Spatial Neophobia |                  |         |   |  |  |
|-------------------|------------------|---------|---|--|--|
| Key               | Code             | Туре    | Description   |  |  |
|                   |                  |         | Time from start of trial for sparrow to enter<br>new cage. Time started at the beginning of<br>trial after the researcher exited the room and |  |  |
|                   | Latency to enter |         | stopped when sparrow crossed the divider  |  |  |
| n                 | new cage         | State   | with whole body.  |  |  |
|                   |                  |         | Total time spent in new cage. Time started<br>every time sparrow crossed divider to enter   |  |  |
|                   | Duration in new  |         | new cage and stopped every time the sparrow   |  |  |
| d                 | cage             | State   | crossed divider to return to home cage.   |  |  |
|                   |                  |         | lotal number of times sparrow crossed   |  |  |
|                   | Number of visits | Doint   | divider with whole body and entered new   |  |  |
| Objec             | number of visits | Font    | Cage.   |  |  |
| Kev               | Code             | Type    | Description   |  |  |
| ,                 |                  | - 5 F - | Time from start of trial for sparrow to   |  |  |
|                   |                  |         | approach food dish. Time started at the   |  |  |
|                   |                  |         | beginning of trial after the researcher exited  |  |  |
|                   | Latency to       |         | the room and stopped when sparrow was   |  |  |
|                   | approach food    |         | close enough to be able to feed from food   |  |  |
| а                 | dish             | State   | dish.   |  |  |
|                   |                  |         | Time from start of trial for sparrow to feed  |  |  |
|                   |                  |         | from food dish. Time started at the beginning   |  |  |
|                   |                  |         | of trial after the researcher exited the room   |  |  |
| f                 | Latency to feed  | State   | head and pecked at food   |  |  |
| 1                 | Latency to reed  | State   | neau anu peereu at 100u.  |  |  |

#### et al., 2020). None of the objects exceeded the size of the food dish.

# 2.3. Behavior analyses

Behavior was measured using BORIS 7.10.2 (Friard and Gamba, 2016). For spatial trials, each video was observed for the latency to enter the novel environment, total amount of time spent in the novel environment, and number of entries into the novel environment. For object trials, each video was observed for the amount of time it took for sparrows to approach and feed from their food dish during control trials or when novel objects were present. Ethograms were created to associate keys with either point-type behaviors (e.g., number of new cage entries) or state-type behaviors (e.g., latency to feed) (Table 1). Each individual's response across behavior trials were averaged for subsequent analyses (e.g., the three novel object trials were averaged).

### 2.4. Statistics

Neither spatial nor object responses were normally distributed (Shapiro-Wilk tests, both p < 0.049; see Fig. 4), therefore the relationship between spatial neophobia and object neophobia was examined using Spearman's rank order correlation analysis in R Studio v 4.3.0 (R Core Team, 2020). Spearman's rank order coefficients were calculated for each pair of spatial and object behaviors within and between contexts. P-values were corrected for multiple testing using the Holm-Bonferroni method (Holm, 1979). To determine the distribution of spatial and object neophobia measures, we created histograms using the "hist" function in R. Cox proportional hazard models were used to investigate patterns in object and spatial neophobia behavior using the "coxme" function in the coxme package (Therneau, 2020). There was no effect of sex (both z > 0.72, p > 0.31), presentation order (both z > 1.84, p > 0.065), or trial date (z > 1.67, p > 0.094) on object or spatial responses, therefore these variables were not included in the final models. To compare neophobia responses to different novel objects and to check for side bias for spatial neophobia, we created Kaplan-Meier survival curves (Therneau, 2021) and used pairwise comparisons, as done previously (Kelly et al., 2020; Kimball et al., 2022). We calculated



**Fig. 2.** House sparrows (n = 23) took significantly longer to feed in the presence of novel objects compared to control conditions (all p < 0.0004). Kaplan-Meier survival curves of house sparrow feeding likelihood in the presence of a novel object on, in, around, or above the food dish (colored lines) or control conditions (regular food dish with no objects; black line). Latency to feed did not differ among the different novel objects (post-hoc comparisons all p > 0.18).

ANOVA-based repeatability (Lessells and Boag, 1987) of individual responses to object and spatial trials using the "rpt.aov" function from the "rptR" package (Stoffel et al., 2017).

#### 3. Results

All novel object responses were significantly different from control responses (Fig. 2; all z < -3.52, all p < 0.001). There was no effect of side (right or left) on latency to enter (z = -0.25, p = 0.8) or duration spent (z = 0.84, p = 0.4) in a novel environment. Object neophobia measures were significantly correlated, with an individual's average latency to feed in the presence of a novel object positively associated with its average latency to approach the food dish when a novel object was present (Fig. 3A; Spearman's correlation = 0.91, p < 0.001). The two spatial neophobia measures were also significantly correlated, with an individual's average latency to enter a new cage negatively associated with the average time it spent in that novel cage (Fig. 3B; Spearman's correlation = -0.94, p < 0.001). These correlations remained significant after Holm-Bonferroni correction. There were no significant correlations between any of the object and spatial measures (Table 2; Fig. 3C-F). Histograms showed bimodal distributions in sparrow behavioral responses for both latency to enter a novel cage and latency to feed in the presence of novel objects (pooled data from individual trials; Fig. 4). Individual responses were slightly more repeatable during object trials (r = 0.55, p < 0.001) than during spatial trials (r = 0.44, p = 0.014).

#### 4. Discussion

It seems logical that a bird that is cautious to enter and explore a novel environment would also be cautious to approach and feed near a novel object, because both contexts involve perception of visual information and decision making about possible risks and rewards. However, we did not find support for this association: an individual's response to a novel object near the food dish was not predictive of its response to a novel environment. This finding is consistent with other studies that have compared novel environment and novel object responses (Fox and Millam, 2007; Martins et al., 2007; Ruuskanen and Laaksonen, 2010), but note that some studies have found correlated responses (Cole and Quinn, 2014; Schuett et al., 2012, 2011; Verbeek et al., 1994). Interestingly, we did find that object and spatial neophobia responses were both bimodally distributed, indicating somewhat distinct behavioral phenotypes for both types of trials.

Why are spatial neophobia and object neophobia correlated in some species and not in others? Positive correlations between two tested behaviors can arise for two different reasons: either because the tests measure the same trait (i.e., the tests have convergent validity), or, alternatively, because the two behaviors are linked as part of an underlying behavioral syndrome (Carter et al., 2013; Sih et al., 2004). Although it is possible that these two different types of neophobia tests may have convergent validity in some species and not others, it seems more likely that the tests we used measure two different traits that may be linked via a behavioral syndrome in some species and not others. There may also be inconsistencies in findings between studies because of differences in neophobia paradigms used. For example, some studies use forced entry into the novel environment and then measure exploration (Boogert et al., 2006; Schuett et al., 2012), whereas others, including this study, allow for choice of entry (Fox and Millam, 2007; Schuett et al., 2011). Additionally, some paradigms include novel objects like unfamiliar perches in the novel environment, which may confound results by unintentionally eliciting object neophobia. Different paradigms may not be comparable because slightly different designs may assess exploration or boldness (Cole and Quinn, 2014; Cortez Ghio et al., 2016; De Meester et al., 2022).

Our novel object paradigm involved a potential approach-avoidance conflict (positive stimulus of the food, potentially negative stimulus of the object) that was distinct from the approach-avoidance conflict present in novel environment trials. Because there was no food reward for entering the novel environment, it is possible that birds would have to find exploring a novel environment to be inherently rewarding in order



Fig. 3. Correlations between average individual spatial and object neophobia measurements in wild-caught house sparrows tested in the lab (n = 23). The gray area represents the 95% confidence interval.

to outweigh any potential risks. Thus, the spatial neophobia paradigm may not be measuring neophobia, but instead neophilia. For a novel object paradigm, neophobia and neophilia can be distinguished by standardizing individual motivation to approach the object (Greenberg and Mettke-hofmann, 2001; Mettke-Hofmann et al., 2009, 2002). If a novel object is placed near a food dish and all individuals have been fasted, motivation is standardized and latencies will be specific to object avoidance (neophobia). Conversely, if a novel object is placed randomly in the animal's environment and there is no standardization of motivation, an individual's inherent interest in something novel will be measured (neophilia). For our spatial neophobia paradigm, motivation was not standardized and there was no incentive (like food) to enter the new environment. Therefore, motivation to avoid the novel environment could be interpreted as neophobia, and motivation to enter could be interpreted as neophobia, and motivation to enter could be interpreted as neophilia (Mettke-Hofmann et al., 2009). To further test this possibility, we could assess whether latency to approach a novel

#### Table 2

Correlation matrix between average spatial and object neophobia measures for each individual house sparrow (n = 23). The first value is Spearman's correlation coefficient and the second value (in italics and parentheses) the associated probabilities. Significant correlations are bolded.

| Behavior<br>measure | Latency to<br>enter novel<br>environment | Time spent in<br>novel<br>environment | Latency to<br>approach<br>novel object | Latency to<br>feed with<br>novel<br>object |
|---------------------|--|---------------------------------------|--|--|
| Latency to          |  |                                       |  |  |
| enter novel         |  | -0.94                                 | -0.079                                 | -0.21                                      |
| environment         | _  | (<0.001)                              | (0.72)                                 | (0.33)                                     |
| Time spent in       |  |                                       |  |  |
| novel               |  |                                       | 0.11                                   | 0.20                                       |
| environment         | _  | _                                     | (0.60)                                 | (0.35)                                     |
| Latency to          |  |                                       |  |  |
| approach            |  |                                       |  | 0.91                                       |
| novel object        | _  | _                                     | _                                      | (<0.001)                                   |

A)





Latency to feed with novel object (seconds)

**Fig. 4.** Histograms showing bimodal distributions of house sparrow behavior data for A) spatial and B) object neophobia (n = 23 sparrows). Data are pooled from all individuals in all trials (n = 46 total spatial trials, n = 69 total object trials).

object in the absence of food is correlated with latency to enter a novel environment in house sparrows. Because different individuals may also differ in how rewarding they find food as a stimulus, it would also be useful to assess neophobia by standardizing test subjects' motivation using other kinds of positive stimuli, such as access to nest sites (Lendvai et al., 2011).

Because spatial neophobia (or perhaps neophilia) was not correlated with object neophobia, we conclude that these two tests do not measure the same underlying trait in house sparrows. We have previously shown

that initial novel object responses, habituation to a novel object, and novel food responses are correlated in house sparrows, and are therefore all measurements of neophobia behavior (Kimball et al., 2022). The wide individual variation we observed in both novel object and novel environment responses may be controlled by distinct functional circuits in the brain. It would be interesting to explore possible neural substrates underlying these different responses using techniques like RNAseq and receptor labeling in areas of the brain linked with novel spatial and object responses, like the hippocampus (Damphousse et al., 2022; Kimball et al., 2022; Lattin et al., 2022). Ultimately, this study demonstrates that animals' responses to different types of novelty are not always consistent. Consistency may be increased by standardizing motivation across different testing paradigms, but this remains to be tested. Certainly, we would encourage researchers interested in neophobia to be thoughtful about how they assess this important behavioral trait, and, whenever possible, think about using multiple testing paradigms and rejecting those that do not show convergent validity.

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#### CRediT authorship contribution statement

Melanie G. Kimball: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing – original draft. Christine R. Lattin: Conceptualization, Methodology, Funding acquisition, Supervision, Writing – review & editing.

#### **Declaration of Competing Interest**

We declare we have no competing interests.

#### **Data Availability**

I have shared data file at the Attach File step.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2023.104913.

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