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Eurasian tree sparrows are more food neophobic and habituate to novel objects more slowly than house sparrows

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Abstract Most research on the variables that allow for introduced species to succeed and become invasive has focused on environmental and ecological factors. Fewer studies have assessed the roles of behavioral and cognitive traits. To help fill this knowledge gap, we studied neophobia, aversive behavior towards novelty, in the non-native Eurasian tree sparrow (*Passer montanus*), and compared results to previous work in a more successful invasive congener, the house sparrow (*Passer domesticus*). We assessed the neophobia of wild-caught Eurasian tree sparrows by measuring their responses to novel objects and novel foods and their ability to habituate to initially novel objects. We predicted that Eurasian tree sparrows, as less successful invaders, would overall be more neophobic than house sparrows. Although we did not observe differences in neophobia towards novel objects in the two species, Eurasian tree sparrows were significantly less willing than house sparrows to try novel foods. Eurasian tree sparrows were also slower to habituate to repeated presentations of the same initially novel object compared to house sparrows. Multiple factors certainly influence invasion success, but our results suggest that neophobia might limit the success of an introduced species in novel environments.

Resumen La mayoría de la investigación sobre las variables que permiten a las especies introducidas tener éxito convertirse en invasoras se ha centrado en factores ambientales y ecológicos. Menos estudios han evaluado los papeles de los rasgos conductuales y cognitivos. Para ayudar a llenar este vacío de conocimiento, estudiamos la neofobia, el comportamiento aversivo hacia la novedad, en el gorrión molinero (Passer montanus) no nativo, y comparamos los resultados con trabajos previos en un congénere invasor más exitoso, el gorrión común (Passer domesticus). Evaluamos la neofobia del gorrión molinero capturados en la naturaleza midiendo sus respuestas a objetos y alimentos nuevos, así como su capacidad para habituarse a objetos inicialmente novedosos. Predijimos que los

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gorriones molineros, como invasores menos exitosos, en general serían más neofóbicos que los gorriones comunes. Aunque no observamos diferencias en la neofobia hacia objetos nuevos en las dos especies, los gorriones molineros fueron significativamente menos dispuestos a probar nuevos alimentos que los gorriones comunes. Además, los gorriones molineros fueron más lentos en habituarse a presentaciones repetidas del mismo objeto inicialmente novedoso en comparación con los gorriones comunes. Sin duda, varios factores influyen en el éxito de la invasión, pero nuestros resultados sugieren que la neofobia podría limitar el éxito de una especie introducida en entornos novedosos.

Résumé La plupart des recherches sur les variables qui permettent aux espèces introduites de réussir et de devenir envahissantes ont principalement porté sur des facteurs environnementaux et écologiques. Moins d'études ont évalué les rôles des traits comportementaux et cognitifs. Dans ce projet, nous avons étudié la néophobie, comportement aversif envers la nouveauté, chez le moineau friquet (Passer montanus), une espèce allochtone en Amérique du Nord, et avons comparé les résultats à ceux obtenus dans un congénère allochtone plus réussi, le moineau domestique (Passer domesticus). Nous avons évalué la néophobie des moineaux friquets en mesurant leurs réponses à des objets et des aliments nouveaux, ainsi que leur capacité à s'habituer à des objets initialement nouveaux. Nous avons prédit que les moineaux friquets, étant des envahisseurs moins réussis, seraient globalement plus néophobes que les moineaux domestiques. Bien que nous n'ayons pas observé de différences de néophobie envers les objets nouveaux entre les deux espèces, les moineaux friquets étaient moins disposés que les moineaux domestiques àn manger des aliments nouveaux. Les moineaux friquets étaient également plus lents à s'habituer à des présentations répétées du même objet initialement nouveau par rapport aux moineaux domestiques. De nombreux facteurs influencent le succès des espèces envahissantes, mais nos résultats suggèrent que la néophobie pourrait limiter le succès d'une espèce introduite dans de nouveaux environnements.

Keywords Neophobia · Invasive species · *Passer montanus* · *Passer domesticus* · Behavioral flexibility · Invasion biology

Palabras clave la neofobia · las especies invasoras · *Passer montanus* · *Passer domesticus* · la flexibilidad conductual · la biología de la invasión

Mots-clés **la** néophobie · les espèces envahissante · *Passer montanus* · *Passer domesticus* · la flexibilité comportementale · les invasions biologiques

Introduction

Invasive species are one of the main threats to biodiversity globally (e.g., Molnar et al. 2008; Clavero et al. 2009; Dueñas et al. 2021). By studying the introduction and spread of non-native species, researchers have identified several variables that allow for their establishment and long-term success. Determining such variables can inform predictions of where and how introduced species may become invasive. So far, most research has focused on environmental and ecological factors that allow an introduced species to succeed, such as climate and habitat matches from native to invaded areas (Hayes and Barry 2008); enemy release from native predators, pathogens, and parasites (Liu and Stiling 2006); and the ability of invasive species to outcompete and exclude native species (Bennett et al. 2011). Fewer studies, however, have assessed how behavioral and cognitive traits may contribute to the success of invasive species, despite a growing literature that suggests a significant role for these types of traits (Chapple et al. 2012; Sol and Maspons 2016; Szabo et al. 2020).

Neophobia, an aversive response towards novelty, is a key behavioral trait that underlies many exploration-avoidance decisions (Greenberg 2003) and may contribute to invasion success. For introduced species, most stimuli, from food sources to nesting sites, are at least somewhat novel upon their introduction. As individuals encounter novel stimuli, they make decisions about possible risks (e.g., exposure to predators or pathogens) and rewards (e.g., access to available resources) that can ultimately impact their fitness (Realé et al. 2007). Previous work has shown that successful invaders tend to be less neophobic than individuals from non-invasive populations or species (e.g., *Rhinella marina* (cane toad) in Candler and Bernal 2015; *Podarcis* lizards in Damas-Moreira et al. 2019; *Acridotheres tristis* (common myna) in Cohen et al. 2020). However, fewer studies have compared behavioral traits of two closely related species that are both invasive but show different degrees of invasion success.

To help fill this knowledge gap, we studied neophobia in non-native Eurasian tree sparrows (*Passer montanus*). Eurasian tree sparrows were introduced to the United States in Saint Louis, Missouri in 1870 (Widmann 1889; Moulton et al. 2010). Despite being successfully introduced less than twenty years after their more familiar and ubiquitous congener, the house sparrow (*Passer domesticus*, which was successfully introduced in Brooklyn, New York in by 1853; Robbins 1973), Eurasian tree sparrows have not invaded nearly as far nor as widely. Eurasian tree sparrows remain restricted to mainly rural areas of a few midwestern states, where they spread from their single successful introduction event of twenty individuals in St. Louis, Missouri (Widmann 1889). In contrast, house sparrows invaded urban and rural portions of the Americas due to numerous successful introductions of individuals sourced from native Eurasian populations and translocations of established American individuals (Robbins 1973; Moulton et al. 2010). These multiple introduction events, and thus higher genetic diversity of introduced populations, have likely contributed to the house sparrow's success in North America (Kolbe et al. 2004; Dlugosch and Parker 2008). Despite the house sparrow's numerous introduction events, propagule pressure (i.e., "introduction effort," see Lockwood et al. 2005) alone is not sufficient to explain the outcomes of bird introductions (Moulton et al. 2013; Moulton and Cropper 2019).

Beyond propagule pressure, certain ecologically relevant behavioral traits could contribute to a species' establishment and spread; however, our understanding of how these traits impact invasion success remains limited. Individual and population-level variation in neophobia is one such behavioral trait that may affect a species' invasion process and outcome. Such variation could be important as less neophobic individuals may promote range expansion because they are less hesitant to exploit new resources, whereas more neophobic individuals may ensure the core population's survival as their fear of novelty keeps them from succumbing to unfamiliar threats in a novel landscape (Greenberg 2003). In fact, numerous studies of house sparrows have documented wide variation in individual responses to novel objects and foods, such that many populations show bimodal distributions with distinct groups of neophobic and non-neophobic birds (Martin and Fitzgerald 2005; Ensminger and Westneat 2012; Liebl and Martin 2014; Kimball et al. 2022). However, such variation has not yet been examined in Eurasian tree sparrows. Ultimately, these species' differential invasion successes and close taxonomic relationship make them an ideal study system for comparisons that explore how behavioral traits like neophobia may influence the outcomes of introduced species.

To explore whether neophobia is a behavioral trait associated with invasion success, our objectives were: (1) to describe neophobia in wild-caught Eurasian tree sparrows in a laboratory setting by measuring their responses to novel objects and novel foods as well as their ability to habituate to the same initially novel object upon repeated exposures, and (2) to compare trends and variation in neophobia of Eurasian tree sparrows to similar existing data from house sparrows. We predicted that Eurasian tree sparrows, as less successful invaders, would be more neophobic in response to novel objects and foods and slower to habituate to novel objects than house sparrows. Furthermore, we also predicted that, on a population level, Eurasian tree sparrows would have less individual variation in neophobia than house sparrows, and thus, show a unimodal distribution in neophobia rather than the bimodal distribution described in house sparrows (Kimball et al. 2022).

Methods

Sparrow capture and processing

We captured adult Eurasian tree sparrows (*Passer montanus*, $n=24$) during daylight hours within the core of their non-native range at a private property in a rural portion of Tazewell County, Illinois, United States in March 2023 using mist nets ($n=15$) and nest box traps ($n=9$). After capture, we banded each sparrow with a uniquely numbered aluminum band and measured their body mass using a digital platform scale (American Weigh Scales, accurate to ± 0.1 g). After processing, we placed sparrows in a modified pet carrier outfitted with food dishes containing millet, water dishes, and multiple perches. Sparrows were housed in the carrier for no longer than 6 h, and no more than 12 sparrows were held at a time. Sparrow capture and the following methods were in accordance with Ornithological Council guidelines (Fair et al. 2023).

Sparrow housing, transportation, and care

At the end of each field day, we transferred sparrows to temporary housing cages at a local field station. Sparrows were singly housed in these cages while field work (i.e., capturing enough sparrows) was ongoing, but they could see and hear each other. Each cage was equipped with two plastic perches, ad libitum water and food (a mix of millet, a vitamin-rich food supplement (Mazuri), and grit), and a live cedar branch to serve as a hide and provide additional perches. These temporary cages were placed in a room with two large windows that allowed the sparrows to experience a natural light–dark cycle, which at the time of capture was approximately 12.5 h light:11.5 h dark. Once we captured all 24 sparrows, we allowed them to acclimate to captivity for at least 48 h before transport to Louisiana State University. We placed 12 sparrows in each of two carriers (each measuring at least 66 cm long, 40 cm wide, and 46 cm heigh) containing food, water, perches, and absorbent padding and drove them overnight to reduce transportation stress (following recommendations from National Research Council 2010; Fair et al. 2023).

Upon arrival at Louisiana State University, we transferred sparrows to long-term housing cages. These cages were equipped with multiple perches of different materials, a tray with sand for dust bathing, a plastic pine branch to serve as a hide, and ad libitum food (a mix of millet, wild bird seeds, Mazuri, and grit) and tap water. The room where the sparrows were housed maintained the light–dark cycle that they experienced at capture using artificial lighting set on a timer. We allowed sparrows to acclimate to captivity for three weeks before beginning behavioral trials. Sparrows were doubly housed until three days before the start of behavioral trials; we then singly housed the sparrows to avoid potential effects of social interactions on neophobia (Kelly et al. 2020). Sparrows were monitored daily for health and had their food and water changed daily by our research team and animal husbandry staff. Throughout their time in captivity, we weighed each sparrow every two weeks to track changes in their mass and ensure that weight loss did not exceed 15% of their body mass at capture.

Neophobia trials

We quantified Eurasian tree sparrow neophobia using the same methods as Kimball et al. (2022), which assessed neophobia in house sparrows (*Passer domesticus*). Briefly, we defined neophobia as the latency (in s) to approach and feed from a dish with a novel object or novel food present. Behavioral trials lasted 1 h, after which the normal food dish was returned for the rest of the day. To standardize motivation to feed, we fasted sparrows overnight from 30 min before lights off until 30 min after lights on (13.5 h total). This period only represents at most an additional 2 h of fasting beyond the normal overnight fast (Lattin et al. 2022). We recorded the sparrows' behavior using an array of pole-mounted security cameras (ZOSI Z18.5.T.2) connected to a DVR (ANNKE Model DM310). Sparrows were not able to see one another during the experiment, but they could hear other individuals.

As in Kimball et al. (2022), we tested object neophobia, food neophobia, and habituation to multiple presentations of the same initially novel object. These experiments lasted three weeks; daily trials to measure object neophobia were performed in week one, food neophobia was measured in week two, and habituation was quantified in week three. Each sparrow served as its own control; at least once during each week of trials, we presented the sparrow with its normal food dish with the standard food mix. Latency to feed from the normal food dish without a novel object was the control condition. Two control trials were conducted for both the object neophobia experiment and the food neophobia experiment, whereas only one control trial was conducted during the third week's novel object habituation experiment. The presentation order of control and treatment conditions for novel object and novel food trials were randomized for each bird during the first two weeks' experiments, but all control trials occurred on day 1 of the novel object habituation experiment. The novel objects and foods used in this study were chosen for several reasons: the sparrows were unlikely to have encountered them in the wild, they have been used previously to induce neophobia in house sparrows (Martin and Fitzgerald 2005; Kelly et al. 2022; Kimball et al. 2022), and they represent a diversity of colors, shapes, textures, and, for foods, flavors (Greggor et al. 2015).

During novel object trials, we planned to present sparrows with four of the five novel objects used previously in house sparrows (Kimball et al. 2022); one of these five objects was reserved for novel object habituation trials in week three. These objects were: a purple plastic egg placed in the food dish, a white cover over part of the dish, a red-painted dish, yellow coiled pipe cleaners around the edge of the dish, and a blinking light hanging above the dish (Figure S1). However, due to a video recording error on one day during the novel food trials of this week, we lost data for one object per sparrow (which was randomly determined at the start of the experiment for each sparrow). In total, we collected data for each sparrow from two control trials (no objects presented) and three novel object trials.

We assessed food neophobia during week two in a similar manner as object neophobia in week one. Sparrows received the same four novel foods as in Kimball et al. (2022), which were: peanut butter, fruit-flavored breakfast cereal, grated cheddar cheese, and chopped kiwi fruit. Each morning, we gave the sparrows approximately the same volume (~ 120 mL) of these foods. During this week, sparrows received two control trials and four novel food trials.

In the final week, we assessed habituation to whichever novel object each sparrow had not seen in week one (which was randomly determined for each individual). We began this week by giving each sparrow their normal food dish as the control condition. On day two of this week, we presented each sparrow with a novel object. We continued to present that same object during each morning trial through day five of this week (i.e., four consecutive days total with the same object).

Because they are an invasive species in North America, Eurasian tree sparrows could not be released after project completion. Therefore, three weeks after the end of behavioral trials, Eurasian tree sparrows were euthanized using an overdose of isoflurane anesthesia followed by rapid decapitation, an approved method according to the 2020 American Veterinary Medical Association Guidelines for the Euthanasia of Animals. We determined each sparrow's sex by examining gonads within the body cavity; gonads were enlarged and distinguishable because we captured sparrows at the beginning of their breeding season. Based on these dissections, our sample size per sex included 13 males and 11 females.

House sparrow neophobia data

Behavior data from house sparrows was used to compare neophobia in these two species. Object neophobia, food neophobia, and novel object habituation were assessed using the same methods described above, as published previously (Kimball et al. 2022). To do so, adult house sparrows ($n=22$, 15 males and 7 females) were captured within the core of their non-native range from local sites in East Baton Rouge Parish, Louisiana, USA. House sparrows were captured using mist nets in suburban areas during June and July 2019. These house sparrows were housed in the same facility and presented with the same set of novel objects and novel foods as the Eurasian tree sparrows in this study. Novel objects and foods were randomly assigned to each trial and each house sparrow. During their study, Kimball et al. (2022) presented house sparrows with three novel objects during object neophobia trials (with $n=2$ control trials per bird) and reserved one object for habituation trials. The final object in the house sparrow study was used in an object neophobia trial to quantify immediate early gene expression; however, our current study did not conduct the last trial to assess immediate early gene expression, nor did we use house sparrow behavior data from that final trial in this comparison. For the purposes of this study's comparison, each house sparrow saw four of the five novel objects (which were randomly determined), but all five objects were shown to at least some of the house sparrows. For food neophobia trials, Kimball et al. (2022) only presented three of the four possible novel foods to house sparrows (again, with $n=2$ control trials per bird); the final food was retained for a novel food habituation trial, but that never occurred. Thus, each house sparrow only saw three of the four novel foods, but all four foods were presented to at least some of the house sparrows (this, again, was randomly determined). Lastly, during the novel object habituation trials, behavioral data from the third object exposure of the house sparrow study were lost due to a video recording error, whereas all four novel object exposures were successfully completed for Eurasian tree sparrows.

Behavior scoring

Two observers (KJK and EBC) watched video recordings from the three weeks of Eurasian tree sparrow behavioral trials and recorded the first time to approach the food dish and first time to eat from the food dish. Repeatability of video scoring between these observers was calculated using interclass correlation coefficients (ICCs, Wolak et al. 2012) and was high for both approach latency (ICC [95% CI] 0.99 [0.99, 1]) and feeding latency (ICC = 0.99 [0.99, 1]). When sparrows did not approach or feed from the dish, we assigned them a maximum time of 1 h (i.e., 3600 s). We also assigned each sparrow a binary approach and feeding status of either 0 or 1, where 0 indicated that the sparrow did not approach/feed during the 1-h trial and 1 indicated that it did. These binary status codes were used in our Cox regression models (described below) to account for the fact that 3600 s does not represent an actual approach or feed time, rather the failure to do either during the trial. Approach and feeding latencies were highly correlated (all $\rho \geq 0.843$, $p < 0.001$) for all trial types (i.e., object neophobia, food neophobia, and object habituation), so we proceeded using only feeding latency for our analyses.

Data analysis

Eurasian tree sparrow neophobia

We used R v 4.2.3 for all analyses and data visualization (R Core Team 2023). First, we examined correlations between average feeding latencies for each sparrow across all three trial types (i.e., object neophobia, food neophobia, and novel object habituation trials) in a pairwise fashion using Spearman's correlation tests. Next, we assessed whether each sparrow's feeding latencies were repeatable across the four novel objects, which included responses to the three objects presented during object neophobia trials and to the first exposure of the final novel object presented during object habituation trials; we similarly assessed repeatability for individual responses to the four novel foods. We quantified repeatability of individual responses in two ways. First, we calculated the ICCs for novel object trials and novel food trials. Second, we used the "rpt.aov" function from the *rptR* package (Schielzeth and Nakagawa 2013; Stoffel et al. 2017) to calculate repeatability using analysis of variance (ANOVA) methods. Before using this function, we assessed whether the residuals of these ANOVAs would be normally distributed by constructing two simple ANOVA-style linear models using the same variables. Residuals from the novel object trials were normally distributed ($W = 0.98$, $p = 0.26$), but those from the novel food trials were not ($W = 0.85$, $p < 0.001$). Thus, this assumption of this repeatability method was not met in one of our datasets, but we wanted to provide both results so that they can be directly compared to repeatability results from Kimball et al. (2022). All these ANOVAs included sparrow identity as the independent variable and feeding latency as the dependent variable. For both the ICC and rpt.aov analyses of repeatability, we included data from the trials where sparrows failed to feed, because these data points represent an important part of the overall distribution of feeding latencies (i.e., birds that would have fed much later, if at all, had the trial continued beyond 1 h); these individuals were assigned feeding latencies of 3600 s.

We then analyzed Eurasian tree sparrow feeding latencies using Cox proportional hazard models with the "coxme" function from the *coxme* package (Therneau 2020). Our preliminary analysis showed that neither sex (all $p \geq 0.45$) nor presentation order of novel objects or foods (all $p \geq 0.29$; see Results for complete statistics from Cox proportional hazard models for presentation order) affected feeding latency in any experiment. Because different capture methods can create sampling bias in studies of animal behavior (Biro and Dingemanse 2009), we also assessed for an effect of capture method (i.e., mist net versus nest box trap) in Eurasian tree sparrows, but we found no effect of capture method on neophobia (all $p \geq 0.07$). Therefore, we did not include sex, trial number, nor capture method in our final models. As with the correlation tests above, object neophobia data included responses to three novel objects presented during the object trial week and the response to the first exposure of the final novel object during object habituation trials. To determine if our novel objects and foods elicited neophobic responses compared to control conditions, we created models that included object type (for object neophobia trials; control and the five objects), food type (for food neophobia trials; control and the four foods), or trial condition (for object habituation trials; control and object exposure days 1–4) as fixed effects; individual identity as a random effect; and feeding latency as the response variable (three total models, one for each type of neophobia trial). When we detected significant differences from the control conditions, we ran post-hoc tests using the "pairwise_survdiff" function from the *survminer* package (Kassambara et al. 2021) to assess differences in feeding latencies between treatment conditions (i.e., object type, food type, or exposure day within each respective model). We created Kaplan–Meier survival curves of Eurasian tree sparrow feeding latency during each trial type using the "survfit" function from the *survival* package (Therneau and Grambsch 2000; Therneau 2023) and visualized these trends using the "ggsurvplot" function from the *survminer* package (Kassambara et al. 2021).

Comparing neophobia between species

We compared neophobia between Eurasian tree sparrows and house sparrows in two ways. First, we assessed any differences in the proportions of each species that successfully fed during the 1-h trials using two sample Z-tests for proportions. In line with our a priori prediction, we conducted one-sided *Z*-tests to specifically test whether the proportions of Eurasian tree sparrows that successfully fed were lower than those of house sparrows. We performed separate tests for each neophobia experiment (object, food, and habituation) and removed the data from the control trials for each test. For object neophobia and food neophobia trials, we pooled the response data across all novel objects (in one analysis) and all novel foods (in another) rather than running separate tests for each different object or food. We chose to pool these data because we were mainly interested in comparing overall trends in object and food neophobia, rather than responses to specific objects or foods. Furthermore, in previous studies of house sparrow neophobia that have used these same novel objects and foods (see Kimball et al. 2022; Lattin et al. 2022; Kimball and Lattin 2023), none of these objects nor foods seemed to elicit consistent neophobic responses across different samples of sparrows (i.e., the object or food that elicits the strongest response in one study does not always produce the strongest response in other studies). However, for object habituation trials, we did not pool the responses across each exposure. Instead, we ran separate *Z*-tests for each exposure, except for the third exposure because we lacked those data for house sparrows.

Second, we built Cox proportional hazard models for each experiment week in a similar fashion to what was described in the preceding subsection. However, unlike the previous Cox models, these three models included species identity as a fixed effect. Species identity was included as an additive term in our object neophobia and food neophobia models, but in our object habituation models, we tested an interaction between species identity and object exposure. To compare whether and when each species habituated to the initially novel objects, we assessed the β estimates and associated p values for each exposure-by-species combination throughout the weeklong habituation trials. From these statistics, we deemed that a species had habituated to novel objects once responses to that object were no longer statistically different from responses to the control condition. These models were analyzed and visualized following the methods described above.

For any of these models where species identity was a significant predictor of feeding latency, we conducted additional statistical tests to further explore interspecific differences. Here, we tested our predictions that Eurasian tree sparrows were more neophobic and showed less variation in their neophobia than house sparrows by conducting one-tailed Mann–Whitney U tests and Levene's tests ("leveneTest" from *car*; Fox and Weisberg 2019), respectively. We also compared distributions of feeding latencies from non-control trials using one-tailed Kolmogorov–Smirnov tests; again, this test was conducted in line with our prediction that distribution of Eurasian tree sparrow feeding latencies would be more right skewed (i.e., more neophobic) than that of house sparrows. We only considered the responses to novel objects or foods (not controls), and we generally (see exception below for Kolmogorov–Smirnov tests) removed data from birds that failed to feed during the 1-h trial. Similarly to the Z-tests described above, we also pooled the responses to all objects (in one test) or foods (in a separate test) for these tests, except for habituation exposures, which were run separately. We decided to retain data from birds that failed to feed (i.e., coded as 3600 s) for these tests, because right-censored data are still informative in an overall distribution of feeding latency. Furthermore, we did not expect a Kolmogorov–Smirnov test to be as sensitive to these values as the other non-parametric tests.

Results

Eurasian tree sparrow neophobia

Average feeding latencies were correlated when compared pairwise among all three trial types (novel object to novel food: $\rho = 0.67$, $p < 0.001$; novel object to object habituation: $\rho = 0.56$, $p < 0.001$; and novel food to object habituation: $\rho = 0.77$, $p < 0.001$; i.e., individual Eurasian tree sparrows that were quicker to feed in the presence of novel objects were also quicker to consume novel foods and to habituate to a novel object). Average feeding latencies of individual Eurasian tree sparrows were significantly repeatable for all novel objects (ICC [95% CI] = 0.26 [0.07, 0.51]; $R = 0.26$, $p = 0.002$) and novel foods (ICC = 0.41 [0.21, 0.64]; $R = 0.42$, $p < 0.001$). For novel object trials, feeding latency was not affected by object presentation order ($\beta = -0.018$, hazard ratio [HR (95% CI)] = 0.98 (0.88, 1.09), $z = -0.33$, $p = 0.74$). Feeding latencies were significantly higher for novel object treatments when compared to control conditions (Table 1a, Fig. 1). Post-hoc tests revealed significant differences in feeding latencies in response to different objects; in particular, sparrows were faster to feed when exposed to the blinking light than compared to the red dish ($p = 0.004$), purple egg ($p < 0.001$), and yellow pipe cleaners ($p = 0.004$). However, responses to the blinking light were not different from responses to the white cover ($p = 0.098$). There were no other pairwise differences between responses to objects (all other $p \geq 0.10$).

During food neophobia trials, the presentation order of novel foods did not affect feeding latency ($\beta = 0.072$, HR (95% CI) = 1.07 (0.94, 1.23), $z = 1.05$, $p = 0.29$). All novel foods caused a significant increase in feeding latency compared to the control condition (Table 1b, Fig. 2). There were no significant differences in feeding latencies among different novel foods (all $p = 0.97$).

For object habituation trials, each object caused a significant increase in feeding latency relative to the control condition (all $p \geq 0.03$; Table S1). Notably, we found that feeding latency during each exposure of the novel objects was significantly longer than the control condition (Table 1c. Figure 3). Even though all object responses were different from the control, post-hoc tests also revealed that feeding latencies

Table 1 Results from three Cox proportional hazard models of Eurasian tree sparrow ($n = 24$) feeding probability during (a) object neophobia, (b) food neophobia, and (c) novel object habituation trials. Individual identity was included as a random effect in each model along with either (a) object type, (b) food type, or (c) exposure number as fixed effects. Results are reported with respect to control conditions for each trial type

Object/food/trial type	β	Hazard ratio (95% CIs)	z	p
(a) *Object neophobia*				
White cover	−2.20	0.11 (0.053, 0.23)	−5.84	<0.001
Red dish	−2.74	0.064 (0.030, 0.14)	−7.05	<0.001
Purple egg	−3.09	0.045 (0.020, 0.11)	−7.19	<0.001
Blinking light	−1.10	0.33 (0.18, 0.60)	−3.62	<0.001
Yellow pipe cleaners	−3.14	0.043 (0.018, 0.11)	−6.88	<0.001
(b) *Food neophobia*				
Cereal	−6.17	0.0021 (0.0005, 0.0084)	−8.67	<0.001
Cheese	−6.71	0.0012 (0.0003, 0.0054)	−8.89	<0.001
Kiwi	−6.58	0.0014 (0.0003, 0.0060)	−8.78	<0.001
Peanut butter	−6.29	0.0019 (0.0005, 0.0077)	−8.71	<0.001
(c) Object habituation				
First exposure	−4.17	0.015 (0.006, 0.043)	−8.03	<0.001
Second exposure	−2.45	0.086 (0.040, 0.19)	−6.28	<0.001
Third exposure	−1.37	0.25 (0.12, 0.52)	−3.77	<0.001
Fourth exposure	−1.13	0.32 (0.16, 0.67)	−3.04	0.002

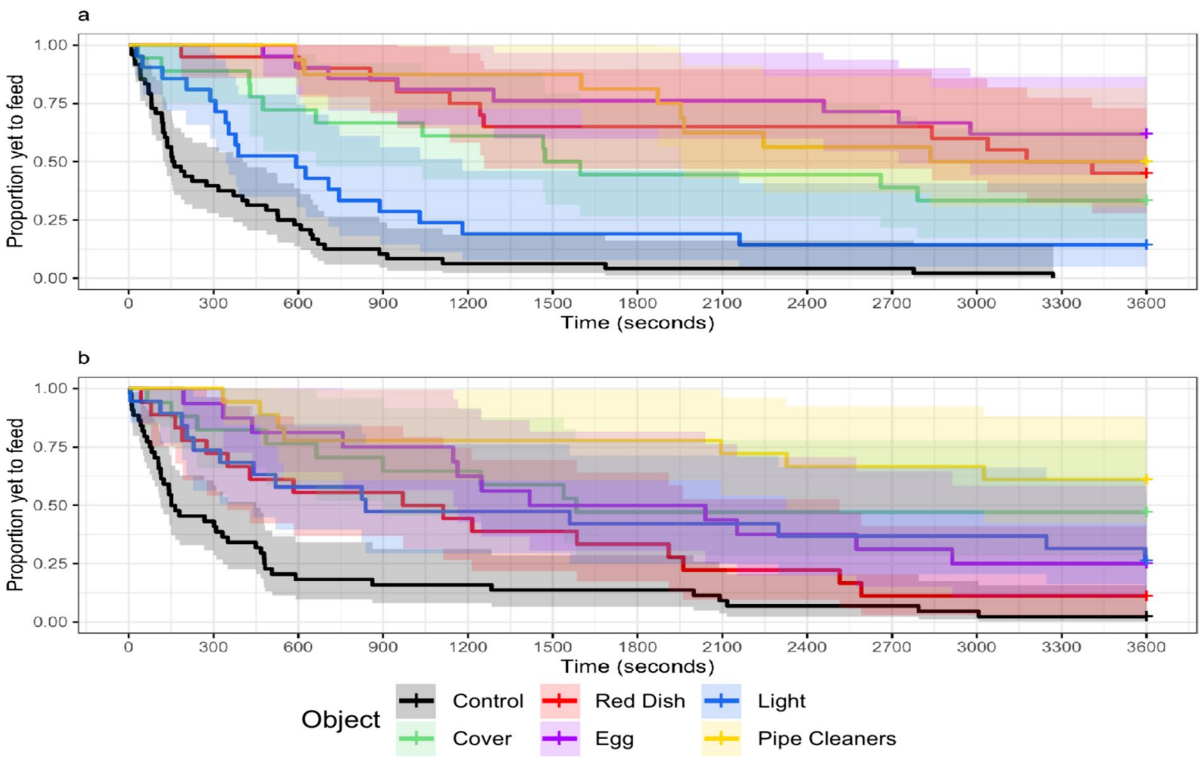

Fig. 1 No apparent differences in object neophobia were detected between **a** Eurasian tree sparrows ($n = 24$) and **b** house sparrows ($n = 22$; house sparrow results from Kimball et al. 2022). Novel objects increased feeding latency relative to the control condition for both species (all $p < 0.001$). Latencies presented here for both species include data from object neophobia trials as well as responses during the first novel object exposure from the object habituation trials. Kaplan–Meier survival curves display the average likelihood of sparrows to feed in the presence of five different novel objects on, in, or near the food dish (colored lines) or in the control condition (i.e., regular food dish with no object; black lines). See main text for details on novel objects used and for post-hoc comparison results for Eurasian tree sparrow responses to different objects

during the third ($p = 0.020$) and fourth ($p = 0.019$) object exposures were significantly shorter than latencies during the first object exposure. There were no other pairwise differences in novel object exposures (all other $p \geq 0.14$).

Comparing neophobia between species

When comparing Eurasian tree sparrows and house sparrows, we first found no differences between the proportion of Eurasian tree sparrows and house sparrows that successfully fed in any trial (object neophobia: $X^2_1 = 0.83$, $p = 0.18$; food neophobia: $X^2_1 = 1.58$, $p = 0.10$; object habituation exposures: all $X^2_1 \leq 0.98$, all $p \geq 0.16$). Similarly, we did not find any differences in feeding latencies between the species during object neophobia trials ($\beta = 0.19$, HR (95% CI) = 1.21 (0.64, 2.30), $z = 0.59$, $p = 0.56$; Table 2a; Fig. 1; Figure S2). However, we did find a difference between the two species' feeding latencies ($\beta = -0.58$, HR (95% CI) = 0.56 (0.34, 0.92), $z = -2.31$, $p = 0.02$; Table 2b; Fig. 2; Figure S3) and the distributions of those latencies ($D = 0.26$, $p < 0.001$; Fig. 4) during food neophobia trials. Specifically, Eurasian tree sparrows were significantly more neophobic towards novel foods than house sparrows ($W = 71$, $p < 0.001$). Despite this, we did not detect interspecific differences in variances of feeding latencies during these trials ($F_{1,\,48} = 0.24$, $p = 0.63$).

Species identity significantly interacted with object exposure number during object habituation trials. Both species' responses during the first two exposures were significantly different from their responses to the control condition (for both species by exposure interactive terms: all $p \leq 0.01$, see Table 2c for all Cox model results; Fig. 3; Figure S4). However,

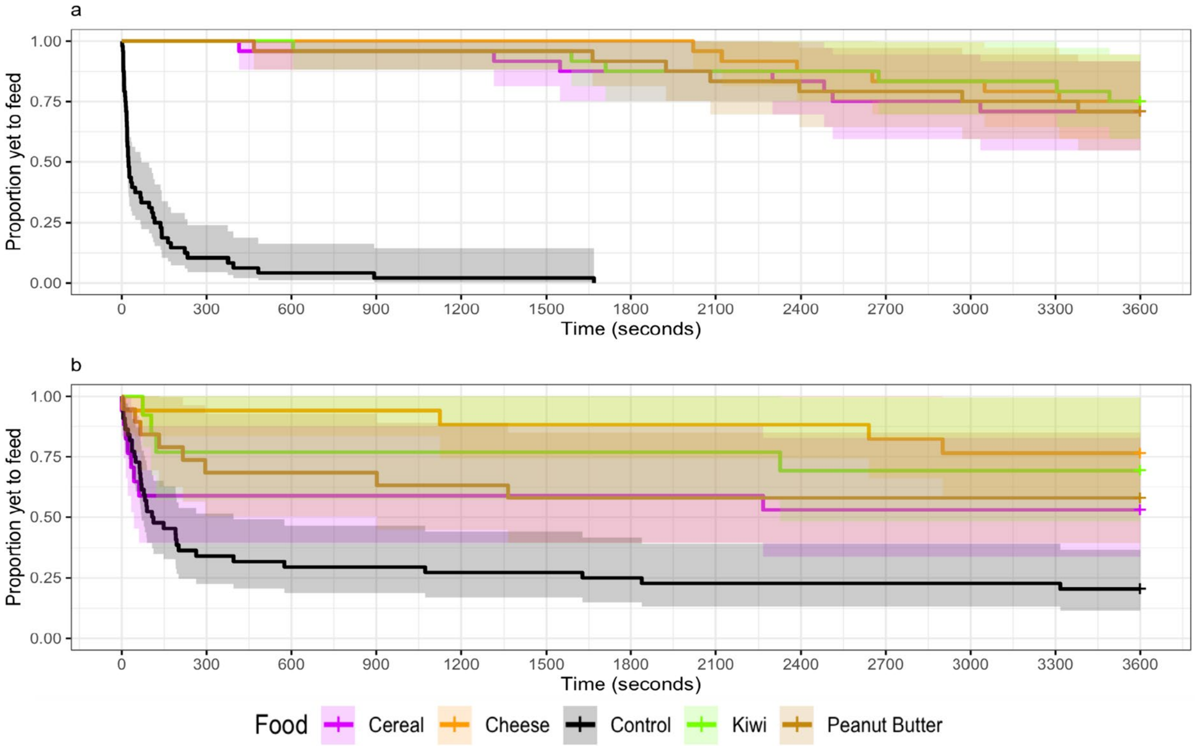

Fig. 2 There were significant differences in feeding latencies between **a** Eurasian tree sparrows ($n = 24$) and **b** house sparrows ($n = 22$) in food neophobia trials. Novel foods increased feeding latency in Eurasian tree sparrows (all $p < 0.001$). However, in house sparrows, feeding latencies only increased from controls for three of the four novel foods ($p \leq 0.002$), because feeding latency for cereal trials did not differ from controls ($p = 0.062$; results from Kimball et al. 2022). Kaplan–Meier survival curves display the average likelihood of sparrows to feed on four different novel foods (colored lines) or the control condition (normal seed mixture; black lines). See main text of this study for details on novel foods used and for post-hoc comparison results of Eurasian tree sparrow responses to different foods

on the fourth exposure, the Eurasian tree sparrows' responses to the novel objects were still different from the control condition ($\beta = -1.27$, HR (95% CI) $= 0.28$ (0.14, 0.58), $z = -3.47$, $p < 0.001$; Table 2c; Fig. 3; Figure S4), but the house sparrows' responses to the objects were no longer different from their control-condition responses ($\beta = 0.90$, HR (95% CI) $= 2.45$ (0.91, 6.64), $z = 1.76$, $p = 0.08$; Table 2c; Fig. 3; Figure S4). Despite these significant differences from the control condition, a post-hoc test did not reveal any significant differences between the species during any exposure event (all $p > 0.28$); thus, the difference exists within each species when considering their object exposure responses relative to their control-condition responses. Furthermore, we did not find any differences between the species' feeding latency distributions (all $D \leq 0.32$, $p \geq 0.17$; Figure S5) or variances (all $F_{1,\ 30} \leq 0.67$, $p \geq 0.42$) for any habituation exposure, nor were there any significant differences in the Mann–Whitney U tests for habituation (all $W \leq 149$, $p \geq 0.23$). Average feeding latency and proportion of birds that successfully fed during each treatment and experiment is shown for each species in Table 3.

Discussion

Our study described behavioral responses to novel objects and foods in the moderately invasive Eurasian tree sparrow and compared its behavior to a highly successful invasive congener, the house sparrow (Sol and Lefebvre 2000; Sullivan et al. 2009). We predicted that Eurasian tree sparrows, as the less successful invader, would behave more fearfully towards novel objects and foods (i.e., be more neophobic), be

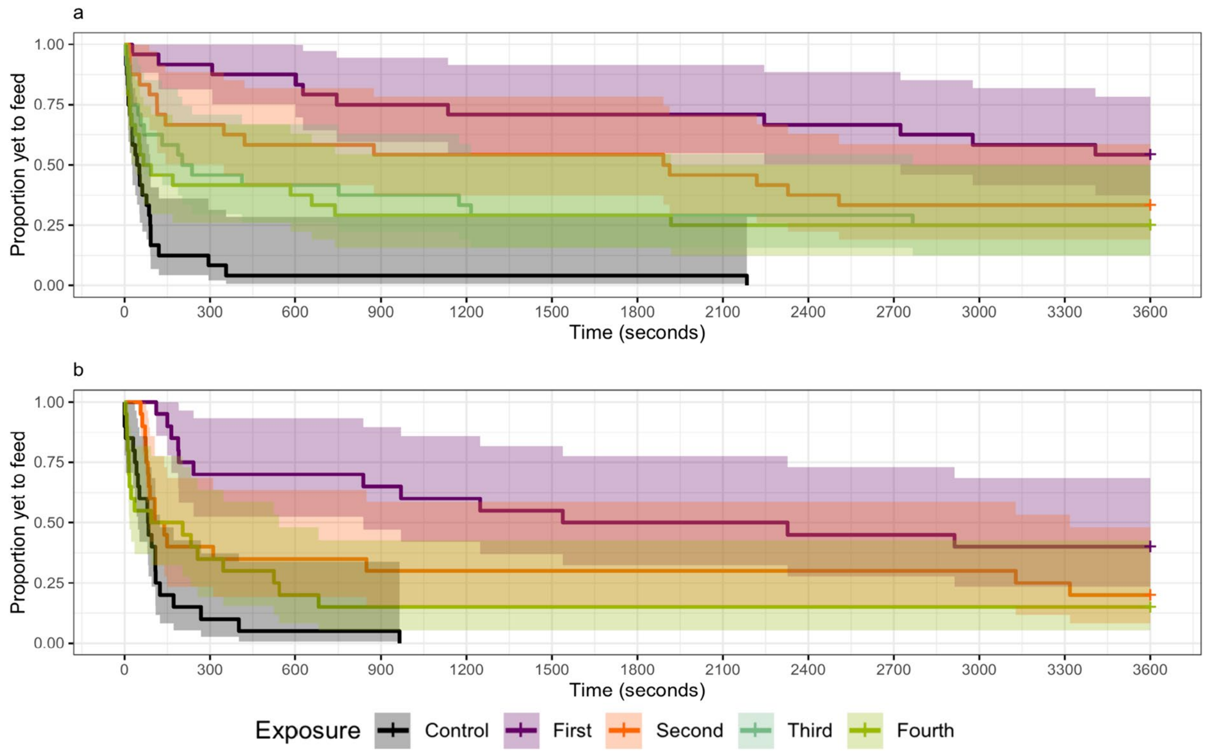

Fig. 3 During novel object habituation trials, **a** Eurasian tree sparrows ($n=24$) did not habituate to the novel object presented, whereas **b** house sparrows ($n=20$, because two individuals were removed from this analysis for failing to feed during the control condition) habituated by the fourth exposure. Feeding latency in response to novel objects initially increased relative to control conditions for both species (both first exposures $p<0.001$). At the end of habituation trials (i.e., during the fourth exposure), feeding latency for Eurasian tree sparrows was still significantly higher compared to the control ($p=0.002$), whereas latency for house sparrows was not different from control latency ($p=0.12$; data from Kimball et al. 2022). Kaplan–Meier survival curves display the average likelihood of sparrows to feed in the presence of an initially novel object that was presented daily for four days (colored lines) and a control condition (no object present; black lines). See the main text for post-hoc comparison results of Eurasian tree sparrow responses to each exposure

less likely to habituate to same initially novel object, and exhibit less among-individual variation in their behavioral responses to novelty when compared to house sparrows. Our predictions were partially supported, as we found that Eurasian tree sparrows were more food neophobic than house sparrows. Eurasian tree sparrows also did not habituate to novel objects during weeklong trials, whereas house sparrows habituated by the fourth object exposure. However, we did not detect any differences in how the two species responded to novel objects presented with familiar food.

Being willing to try unfamiliar foods is essential for the success of introduced species, which may find themselves in environments with few familiar plants, insects, or other food resources. Indeed, low food neophobia and high feeding innovation (or "consumer innovation"), which, in many studies (e.g., Nicolakakis and Lefebvre 2000; Sol and Lefebvre 2000; Cohen et al. 2020), includes the consumption of novel food resources, seem to be common behavioral traits of successful invasive species. For example, previous studies have found that invasive species or individuals at the edge of an invasive population's range are less fearful of novel foods and more willing to consume those foods than native species or invasive individuals within the core of the non-native range, respectively (Sol and Lefebvre 2000; Martin and Fitzgerald 2005; Liebl and Martin 2014; Cohen et al. 2020). An animal's willingness to try a novel food can be impacted by neurobiological and cognitive traits such as sensitivity to sensory inputs (e.g., olfaction), the ability to

Table 2 Results from Cox proportional hazard models of Eurasian tree sparrow and house sparrow feeding probability during novel object (total $n = 276$ trials), novel food (total $n = 254$ trials), and novel object habituation (total $n = 176$ trials) experiments. Species identity was included as a fixed effect in each model in addition to fixed effects of object type, food type, and exposure number for each experiment, respectively. An interaction between species identity and exposure number was tested in the novel object habituation model. Individual identity was also included as a random effect. Data from the third exposure were not compared because the data from this day of the house sparrow trials were lost due to a recording error. Results are reported with respect to control trials and Eurasian tree sparrows as the reference category

Predictor variable	β	Hazard ratio (95% CIs)	z	p
(a) Object neophobia				
Species identity (HOSP)	0.19	1.21 (0.64, 2.30)	0.59	0.56
White cover	−2.12	0.12 (0.07, 0.20)	−7.83	<0.001
Red dish	−2.63	0.07 (0.04, 0.13)	−8.36	<0.001
Purple egg	−1.39	0.25 (0.16, 0.39)	−9.32	<0.001
Blinking light	−3.24	0.04 (0.02, 0.08)	−6.01	<0.001
Yellow pipe cleaners	−2.11	0.12 (0.07, 0.20)	−9.59	<0.001
(b) Food neophobia				
Species identity (HOSP)	−0.58	0.56 (0.34, 0.92)	−2.31	0.02
Cereal	−2.27	0.10 (0.06, 0.19)	−7.25	<0.001
Cheese	−2.88	0.06 (0.03, 0.11)	−7.96	<0.001
Kiwi	−2.78	0.06 (0.03, 0.12)	−7.63	<0.001
Peanut butter	−2.40	0.09 (0.05, 0.17)	−7.75	<0.001
(c) Object habituation				
Species identity (HOSP)	−0.77	0.46 (0.16, 1.33)	−1.43	0.15
Exposure 1	−3.78	0.02 (0.01, 0.06)	−8.33	<0.001
Exposure 2	−2.43	0.09 (0.04, 0.18)	−6.44	<0.001
Exposure 4	−1.27	0.28 (0.14, 0.58)	−3.47	<0.001
Species (HOSP) * Exposure 1	1.43	4.20 (1.39, 12.69)	2.54	0.01
Species (HOSP) * Exposure 2	1.44	4.20 (1.54, 11.50)	2.78	0.005
Species (HOSP) * Exposure 4	0.90	2.45 (0.91, 6.64)	1.76	0.08

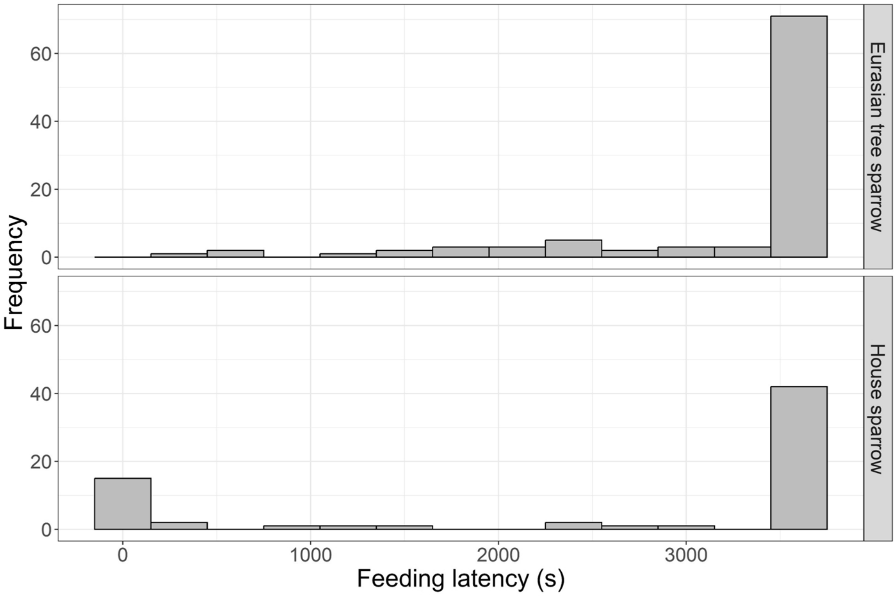

Fig. 4 Distributions of feeding latency of Eurasian tree sparrows (above, $n = 96$ trials) and house sparrows (below, $n = 66$ trials) in response to novel foods during food neophobia trials were significantly different ($D = 0.26$, $p < 0.001$)

Table 3 Average time to feed and proportion of successful trials during (a) object neophobia, (b) food neophobia, and (c) novel object habituation trials for Eurasian tree sparrows ($n=24$) and house sparrows ($n=22$). The control condition in each case was replacing the normal food dish after an overnight fast. Average latencies for successful trials (i.e., sparrows that actually fed during the 1 h trials) are presented for each treatment condition. Threshold values of 3600 s were not included in these averages, because these values signified not feeding during the trial rather than a true feeding time. Therefore, the proportion of birds that fed is also shown. During habituation trials, two house sparrows failed to feed during the control condition, so their data were removed from future trials. Also, due to an error during the third day of object habituation trials for house sparrows, data from that trial were lost

Object, food, or trial type	Average feeding latency ± S.E. (s)		Proportion that fed	
	Eurasian tree sparrow	House sparrow	Eurasian tree sparrow	House sparrow
(a) Object neophobia				
Control	430 ± 93	493 ± 115	48/48 (100%)	43/44 (98%)
White cover	1097 ± 267	763 ± 195	12/18 (67%)	9/17 (53%)
Red dish	1699 ± 353	998 ± 219	11/20 (55%)	16/18 (89%)
Purple egg	1521 ± 365	1365 ± 257	8/21 (38%)	12/16 (75%)
Blinking light	577 ± 121	1027 ± 319	18/21 (86%)	14/19 (74%)
Yellow pipe cleaners	1710 ± 273	1332 ± 412	8/16 (50%)	7/18 (39%)
(b) Food neophobia				
Control	127 ± 40	319 ± 114	48/48 (100%)	35/44 (80%)
Cereal	1943 ± 339	306 ± 280	7/24 (29%)	8/17 (47%)
Cheese	2590 ± 210	1669 ± 678	6/24 (25%)	4/17 (24%)
Kiwi	2229 ± 457	657 ± 557	6/24 (25%)	4/13 (31%)
Peanut butter	2126 ± 357	378 ± 174	7/24 (29%)	8/19 (42%)
(c) Object habituation				
Control	158 ± 90	140 ± 48	24/24 (100%)	20/22 (91%)
First exposure	1356 ± 374	907 ± 272	11/24 (46%)	12/20 (60%)
Second exposure	817 ± 244	544 ± 266	16/24 (67%)	16/20 (80%)
Third exposure	408 ± 166	–	18/24 (75%)	–
Fourth exposure	249 ± 113	177 ± 54	18/24 (75%)	17/20 (85%)

generalize between novel foods and previously consumed items, and learning from conspecific social cues (Kelly et al. 2020; Griffin et al. 2022; McLaughlin and Westneat 2023). There may be differences in these types of traits between house sparrows and Eurasian tree sparrows that make some individual house sparrows more likely to try novel foods. Additionally, if food neophobia has some genetic basis.

(see Crane et al. 2020), the introduction of only twenty Eurasian tree sparrows may have created a founder effect that constrained genetic variation in this trait, or house sparrows living in North America might have been more subject to disruptive selection than Eurasian tree sparrows. Future studies should further investigate the genetic, physiological, and neurobiological mechanisms underlying differences in food neophobia both within and among introduced species.

In addition to interspecific differences in food neophobia, we found that house sparrows habituated to a novel object by the end of our weeklong trials, but Eurasian tree sparrows did not habituate in this same timeframe. The ability to quickly habituate to novel objects that are not dangerous, and which may even provide some sort of benefit (e.g., access to food or nesting habitat), is crucial for a successful invasive species (Greenberg 2003; Griffin et al. 2016). In fact, another widespread invasive species, the European starling (*Sturnus vulgaris*), was shown to habituate to novel objects within just three exposures (de Brujin and Romero 2020). Broader comparisons among multiple invasive species would help to confirm the role that the rate of habituation to novelty plays in invasion success.

Even though house sparrows appeared to habituate to novel objects sooner than Eurasian tree sparrows, we did not find any differences between these species' responses to initial presentations of novel objects. Other studies have similarly found no differences in object neophobia between populations with distinct invasion successes (i.e., native vs. invasive or edge vs. core populations), despite clear differences in these populations' responses to novel foods (Martin and Fitzgerald 2005; Bókony et al. 2012; Liebl and Martin 2014; Cohen et al. 2020; Quesada et al. 2022). On a population level, previous studies suggest that object neophobia is initially lower when a species is first introduced, which likely facilitates their exploration of novel environments; however, neophobia increases once the environment is no longer novel and the population would benefit from wariness towards new threats (Greenberg and Mettke-Hofmann 2001; Echeverría and Vassallo 2008; Wright et al. 2010; Sol et al. 2011). Because house sparrows and Eurasian tree sparrows have been established in the United States for a similar amount of time, any initial differences in object neophobia that may have existed in these populations may no longer be present. Interestingly, although we saw species differences in food neophobia and not in object neophobia, both our study and Kimball et al. (2022) found correlations between object and food neophobia within individuals, suggesting that these behaviors either reflect the same underlying cognitive trait (Carter et al. 2013) or are part of a neophobia behavioral syndrome for both species (Sih et al. 2004).

Lastly, we were interested in how neophobia varied among Eurasian tree sparrows and how that compared to variation in neophobia in house sparrows. Despite no apparent differences in variation in feeding latencies between these species, we found that Eurasian tree sparrows as a group had a more unimodal neophobic response towards novel foods compared to a more bimodal response in house sparrows, which could restrict the ability of Eurasian tree sparrow populations to exploit novel food resources (Sol et al. 2011; Szabo et al. 2020). However, we did not find any differences in the distribution or variation in object neophobia or novel object habituation between these two species. Object neophobia and habituation have been repeatedly described as highly variable among house sparrows (Ensminger and Westneat 2012; Kimball et al. 2022; McLaughlin and Westneat 2023). Our results suggest that populations of Eurasian tree sparrows have a similar amount of individual variation in their initial responses to novel objects and the extent to which they habituate to novel objects. It is currently unclear what generates this within-species individual variation in neophobia, but it may arise partly due to intraspecific genetic variation or learning based on unique experiences with previous forms of novelty.

One limitation to this research is that we indirectly compared these two species, with house sparrows and Eurasian tree sparrows being sampled from different sites, seasons, and years. However, Fischer et al. (2020) found no differences in neophobia in house sparrows at different times of year, and neophobia was similar in house sparrows captured from two core-range populations in Connecticut (Lattin et al. 2022) and Louisiana (Kimball et al. 2022); together, these studies suggest no seasonal or regional effects on house sparrow neophobia in the United States. Although no studies to date have explored if Eurasian tree sparrow neophobia varies across their non-native range, we have done our best to only compare birds of both species from core-range populations (i.e., Eurasian tree sparrows from Illinois and house sparrows from Louisiana). Sampling in this way should have helped to limit any population-level differences in core versus edge birds (Martin and Fitzgerald 2005). Furthermore, we strictly repeated methods for both experimental trials and statistical analyses across both of our studies to reduce sources of error and to produce the best results possible with this type of study design. We also acknowledge that there are limitations to drawing conclusions from two species comparisons (Garland and Adolph 1994). However, to reduce taxonomic variation, we were limited to conducting a two-species study, because house sparrows and Eurasian tree sparrows are the only two members of the genus *Passer* and the family Passeridae in the United States. Future studies should consider directly comparing behavioral and cognitive traits across other taxa where there are closely related species with distinct invasion successes (Jourjine and Hoekstra 2021). Lastly, we recognize that limiting our neophobia trials to one hour prevented us from determining the full range of possible feeding latencies. However, pilot attempts to habituate house sparrows to a feeding grid apparatus to test spatial cognition showed that highly neophobic birds will not feed near a novel object even in trials that last as long as four hours (C.R. Lattin, personal communication). Thus, rather than running very long trials that might impose additional stress on these small songbirds, we chose to right-censor data beyond the one-hour cutoff; this trial duration still provides informative data.

While other factors like life history traits (Cassey 2002), environmental context (Redding et al. 2019), and interspecific competition (Widmann 1889; Cecil 2002) have also likely impacted the successes of these two invasive sparrows, we found evidence that food neophobia and habituation to novelty may be behavioral traits that could partially explain the different invasion successes of these two congeneric songbirds. As non-native species continue to be accidentally and purposefully introduced worldwide, we need a better understanding of how behavioral traits such as neophobia influence their ability to become invasive. Further studies of closely related species with different degrees of invasion success can help us understand the differences between animals that merely survive and those that thrive in new environments.

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Author contributions Kevin J. Krajcir, Tosha R. Kelly, Melanie G. Kimball, Sara E. Lipshutz, and Christine R. Lattin conceptualized the project. Melanie G. Kimball and Christine R. Lattin secured funding for the project. Kevin J. Krajcir, Tosha R. Kelly, and Sara E. Lipshutz conducted fieldwork. Lab work and behavioral assays were performed by Kevin J. Krajcir, Tosha R. Kelly, Melanie G. Kimball, Ella B. Cochran, Keegan R. Stansberry, Blake A. Dusang, Ayushi Patel, and Danna F. Masri. Kevin J. Krajcir, Melanie G. Kimball, and Christine R. Lattin analyzed the data. Kevin J. Krajcir and Christine R. Lattin prepared the original draft of the manuscript. All authors contributed to the review and editing of the finalized manuscript, gave their approval for publication, and agreed to be held accountable for work performed here.

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Data availability Eurasian tree sparrow behavioral data and R code used to analyze the datasets can be accessed from Dryad here: https://doi.org/10.5061/dryad.f4qrfj72h. This work also contains house sparrow behavioral data that were originally published in Behavioural Brain Research, 428, Kimball, M. G., Gautreaux, E. B., Couvillion, K. E., Kelly, T. R., Stansberry, K. R., and Lattin C. R., Novel objects alter immediate early gene expression globally for ZENK and regionally for c-fos in neophobic and non-neophobic house sparrows, 113863, Copyright Elsevier (2022). Those data can be accessed here: https://www.sciencedirect.com/science/article/abs/pii/S0166432822001310?via%3Dihub.

Declarations

Conflict of interest We declare that we have no competing interests.

Ethical approval This study was conducted in accordance with Ornithological Council guidelines and was approved by private landowners, the Louisiana State University IACUC committee (project 10–2021), and the Illinois Department of Natural Resources (permit W23.6844).

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