

Research



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Animal behaviour

No, you go first: phenotype and social context affect house sparrow neophobia

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Novel object trials are commonly used to assess aversion to novelty (neophobia), and previous work has shown neophobia can be influenced by the social environment, but whether the altered behaviour persists afterwards (social learning) is largely unknown in wild animals. We assessed house sparrow (*Passer domesticus*) novel object responses before, during and after being paired with a conspecific of either similar or different behavioural phenotype. During paired trials, animals housed with a similar or more neophobic partner demonstrated an increased aversion to novel objects. This change did not persist a week after unpairing, but neophobia decreased after unpairing in birds previously housed with a less neophobic partner. We also compared novel object responses to non-object control trials to validate our experimental procedure. Our results provide evidence of social learning in a highly successful invasive species, and an interesting asymmetry in the effects of social environment on neophobia behaviour depending on the animal's initial behavioural phenotype.

1. Introduction

Exploration-avoidance behaviour, an individual's reaction to new situations or stimuli [1], has been related to fitness-linked traits such as survival [2,3] and breeding success [2,4]. Although predicting animal range shifts has primarily focused upon physiological constraints to adaptation, cognitive constraints, such as the capacity for social learning, are a likely additional factor limiting future species distributions [5]. Social learning has the potential to help animals avoid dangers and exploit new resources through the rapid transmission of individual innovations [6,7] e.g. horizontal (intra-generational) transmission of information about a novel food source. However, the extent to which wild animals are able to retain information after removal from the social environment is not well understood, despite fitness consequences and possible conservation implications [7,8].

Novel object trials are commonly used to evaluate social effects on individual exploratory behaviour in many taxa, including fish [9–11], mammals [12,13] and birds [14–22]. In a social environment, fish [10,11] and birds [14,19,22] generally behave more similarly to other animals in that environment (social conformity hypothesis [23]) rather than emphasizing individual differences to reduce competition and increase social coordination (social facilitation hypothesis [24]). Few studies, however, consider how interacting with a single individual of a different behavioural phenotype may cause long-term adjustment of an individual's own exploratory response [11,19,22]. To our knowledge, only one study (in rainbow trout, *Oncorhynchus mykiss* [11]) has tested for lasting effects of observing conspecific exploratory behaviour. In this study, pre-assessed 'bold' and 'shy' individuals observed the novel object trial of either a 'bold' or 'shy' conspecific. Observing a bold fish did not change latency to approach a novel object, but bold trout that observed shy individuals increased their latency to approach novel objects when tested up

to 3 days after isolation. This post-observation modulation of exploratory behaviour in the absence of current social cues suggests long-term memory [25] and horizontal transmission of information regarding the novel object—i.e. social learning.

In this study, we tested whether individuals of a highly successful invasive species (i) adjusted neophobia behaviour in the presence of a conspecific; (ii) whether that adjustment depended on the individual's or partner's behavioural phenotype and (iii) whether socially induced changes in neophobia persisted or appeared a week after the partner was removed (evidence of social learning). Here, we use the term 'neophobia', a type of exploratory behaviour [1], to describe a long latency to approach novel objects. The house sparrow (*Passer domesticus*) exhibits wide and repeatable individual variation in neophobia [26–28], making it an excellent system to evaluate the effects of the social environment and different phenotypes on behaviour.

We evaluated the latency of sparrows to approach a novel object before, during and after being paired with a bird of a similar (control) or different phenotype. While social conformity usually refers to a tendency to copy what a majority of others in a group are doing, some authors have suggested that this concept could be extended to paired individuals [29]. Therefore, we predicted that house sparrows would change neophobia behaviour to increase social conformity, similar to observations in other avian species [19,22] and in keeping with research that successful invasive bird species exhibit high behavioural plasticity [30]. Specifically, we predicted neophobic sparrows would become less neophobic when housed in a mixed-phenotype pair, and that non-neophobic sparrows would become more neophobic when housed in a mixed-phenotype pair. We predicted no behavioural change in our matched-phenotype pairings. Considering that house sparrows exhibit social learning of food preferences [31], we also predicted that changes in neophobia would persist after pairs were broken apart. However, in contrast with the previous food preference study, our study tested for impacts of social learning on changes in neophobia in response to new novel objects, instead of repeated exposure to objects previously seen in the social environment. This eliminated the possibility of simply 'copying' behaviours experienced in the social environment and, instead, tested for extrapolation of observed behaviours to a novel experience.

2. Methods

(a) Subject capture and housing

We captured 24 house sparrows (12 males, 12 females) in Iberville and Lafourche Parishes, Louisiana, USA, using mist nets near bird feeders in November 2019. We individually housed sparrows in cages in a vivarium at Louisiana State University with unlimited access to mixed seeds, grit, a vitamin-rich food supplement (Purina Lab Diet for small birds) and water. Light cycle was synchronized with the capture date (10.5 L: 13.5 D) and maintained at this level for the duration of the experiment. Sparrows were visually but not acoustically isolated from one another to prevent observations of their neighbours' novel object trials. Sparrows received an aluminium band with a unique number and were acclimated to captivity for 8–10 weeks until novel object trials began in mid-January.

(b) Study design

This study took place over five weeks. *Week 1, test individual phenotypes*: we exposed individual house sparrows to three randomly selected novel objects and two control days (no object) in a randomized order. *Week 2, assess individual phenotypes and create pairs*: we observed recordings for each sparrow's time to feed on its food dish. Based on average feeding time, we created house sparrow pairs that were similar in approach time (matched-phenotype controls; five pairs; electronic supplementary material, table S1). The remaining birds were paired with a sparrow with a different phenotype (mixed-phenotype pairing; seven pairs; electronic supplementary material, table S1). We introduced pairs to one another in a new cage to reduce the possibility of territoriality. One individual from each pair received a second aluminium band to distinguish individuals in recordings. We acclimated pairs together for 3 days before continuing novel object trials. *Week 3, paired trials*: we exposed pairs to three randomly selected objects, novel to both individuals, and two control conditions in a random order. *Week 4, individual housing acclimation*: we separated pairs and returned individuals to their original cage during the fourth week to allow acclimation before beginning the final novel object exposures. *Week 5, re-test individual phenotypes*: we exposed sparrows to three new novel objects and two control conditions in a random order to test whether having a cage mate had lasting effects on neophobia behaviour (evidence of social learning).

(c) Novel object exposure procedure

Over the five weeks, we exposed sparrows to a total of 15 trials, six controls and nine unique novel objects: a blinking light, a white cover over part of the dish, yellow pipe cleaners, a purple plastic egg, a red-painted dish, a tinfoil hood, three gold bells, pink puffs and an opened blue cocktail umbrella (images in electronic supplementary material). Objects were chosen to maximize the diversity of textures, colours and shapes of novel objects, and all objects were placed on, in, or immediately above the food dish. Sparrows saw each object once. These objects were based on objects shown to elicit delayed approach and feeding in another songbird species [32], but altered slightly to share fewer common features (e.g. red colour) that might incidentally target ecologically relevant cognitive biases [33].

The night before a trial, we removed food dishes from cages 30 min before lights off and fasted sparrows overnight. We replenished seed in the dishes and outfitted them with an object (or no object, for controls). The next morning, 30 min after lights on, researchers entered the room, began a video recording of all cages (12 cameras, two birds per camera), replaced food dishes according to individual treatments and left for 1 h. Researchers were present in the room for less than 4 min. Sparrows were therefore fasted for a total of 15 h (1 h light, 14 h dark) before neophobia or control treatments. This fasting period ensured that sparrows would be motivated to approach the food dish. Upon re-entering the room, the video recording was stopped, and objects removed from food dishes. Videos were scored for the time each sparrow took to eat from the food dish. Two different observers scored all videos. To ensure intercoder reliability, these observers re-watched 14 videos from paired trials ($n = 28$ feeding events) one month later, and ANOVA tests showed no significant differences within ($F_{2,81} < 0.001$; $p = 0.99$) or between ($F_{1,54} < 0.001$, $p = 0.99$) observers.

(d) Statistical approach

We split sparrows into three categories: (i) paired with an individual of similar neophobia response (control; $n = 10$ birds), (ii) paired with a less neophobic individual (partner faster to feed

Table 1. Results of three Cox proportional hazard models of house sparrow feeding probability during control trials (no novel object) for each pairing type. Subject ID was included as a random effect and week as a fixed effect. Contrasts are with respect to week 1 solo trials. See electronic supplementary material for datapoint losses. *n* represents the number of control trials.

week, sample size	β coefficient	hazard ratio (95% confidence interval)	Z-score	<i>p</i> value
control pairs, <i>n</i> = 58				
week 3 (paired), <i>n</i> = 20	−0.41	0.66 (0.34–1.29)	−1.19	0.23
week 5 (unpaired), <i>n</i> = 18	−0.13	0.88 (0.44–1.74)	−0.36	0.72
paired with a less neophobic bird (partner faster to feed), <i>n</i> = 42				
week 3 (paired), <i>n</i> = 14	−0.53	0.59 (0.25–1.37)	−1.24	0.21
week 5 (unpaired), <i>n</i> = 14	0.13	1.13 (0.52–2.49)	0.32	0.75
paired with a more neophobic bird (partner slower to feed), <i>n</i> = 42				
week 3 (paired), <i>n</i> = 14	−0.46	0.63 (0.27–1.47)	−1.07	0.29
week 5 (unpaired), <i>n</i> = 14	−0.05	0.95 (0.43–2.12)	−0.13	0.90

Table 2. Results of three Cox proportional hazard models of house sparrow feeding probability when exposed to a novel object on, in, or above the food dish for each pairing type. Subject ID was included as a random effect, object type as a covariate, and week as a fixed effect. Contrasts are with respect to week 1 solo trials. Significant terms are italicized ($p < 0.05$). See electronic supplementary material for datapoint losses. *n* represents the number of object trials.

week, sample size	β coefficient	hazard ratio (95% confidence interval)	Z-score	<i>p</i> value
control pairs, <i>n</i> = 85				
week 3 (paired), <i>n</i> = 28	−0.67	0.51 (0.24–1.08)	−1.77	0.07
week 5 (unpaired), <i>n</i> = 27	0.13	1.1 (0.62–2.09)	0.42	0.68
paired with a less neophobic bird (partner quicker to feed), <i>n</i> = 62				
week 3 (paired), <i>n</i> = 20	0.51	1.66 (0.82–3.37)	1.42	0.15
week 5 (unpaired), <i>n</i> = 21	<i>0.98</i>	<i>2.66 (1.19–5.95)</i>	<i>2.35</i>	<i>0.02</i>
paired with a more neophobic bird (partner slower to feed), <i>n</i> = 62				
week 3 (paired), <i>n</i> = 20	−1.43	0.24 (0.11–0.53)	−3.47	<0.001
week 5 (unpaired), <i>n</i> = 21	−0.29	0.75 (0.35–1.58)	−0.75	0.45

in the presence of novel objects; $n = 7$ birds) and (iii) paired with a more neophobic individual (partner slower to feed in the presence of novel objects; $n = 7$ birds; electronic supplementary material, table S1). See electronic supplementary material for datapoint losses. We used Cox proportional hazard models to investigate the mere effect of having a cage mate (i) as well as having a cage mate with a different neophobia phenotype (ii and iii) separately using the ‘coxme’ package [34] in R Studio version 3.6.3 [35]. Using a survival analysis approach [36] avoids creating arbitrary threshold values when a subject does not perform the expected behaviour during the allotted time period, which may bias alternative statistical approaches—i.e. giving subjects a time of 3600 s if they do not feed during a 60 min trial. Each model included subject as a random effect, week as a fixed effect and were interpreted as full models. Analyses were performed for control trials (to detect effects of the experimental procedure) and novel object trials (to detect neophobia effects) separately, resulting in six models. Novel object trials also included object as a fixed effect. Because effects of neophobia were detected in models run using novel object trials only, the contrasts among objects were arbitrarily against the object coded as ‘1’, so we do not report these contrasts. Instead, to validate that each object significantly increased latency to feed, we ran a seventh model that included all trials (all individuals, control and object trials). This seventh model included subject as a random effect and object (or not) as a fixed effect.

3. Results

All nine novel objects significantly decreased feeding probability compared to control trials ($n = 351$ trials, all pairing types; all negative β and $p < 0.001$; electronic supplementary material, table S2 and figure S1). The likelihood of feeding was unaffected by having a cage mate during control trials (no object presented), regardless of pairing type (table 1 and electronic supplementary material, figure S2). For novel object trials, there was a marginal negative effect ($p = 0.07$) of having a cage mate with a similar neophobia response on the likelihood of feeding (table 2 and figure 1*a,d*). Being paired with a less neophobic bird increased an animal’s likelihood to feed after pairs were separated but not when paired (table 2 and figure 1*b,e*). By contrast, having a more neophobic partner significantly decreased an animal’s likelihood of feeding while paired, but this effect did not persist after pairs were separated (table 2 and figure 1*c,f*).

4. Discussion

We present the first evidence that a social environment can have long-lasting effects on neophobia (a type of exploratory behaviour) in birds and credit this phenomenon to social learning. The latency of this effect after social experiences

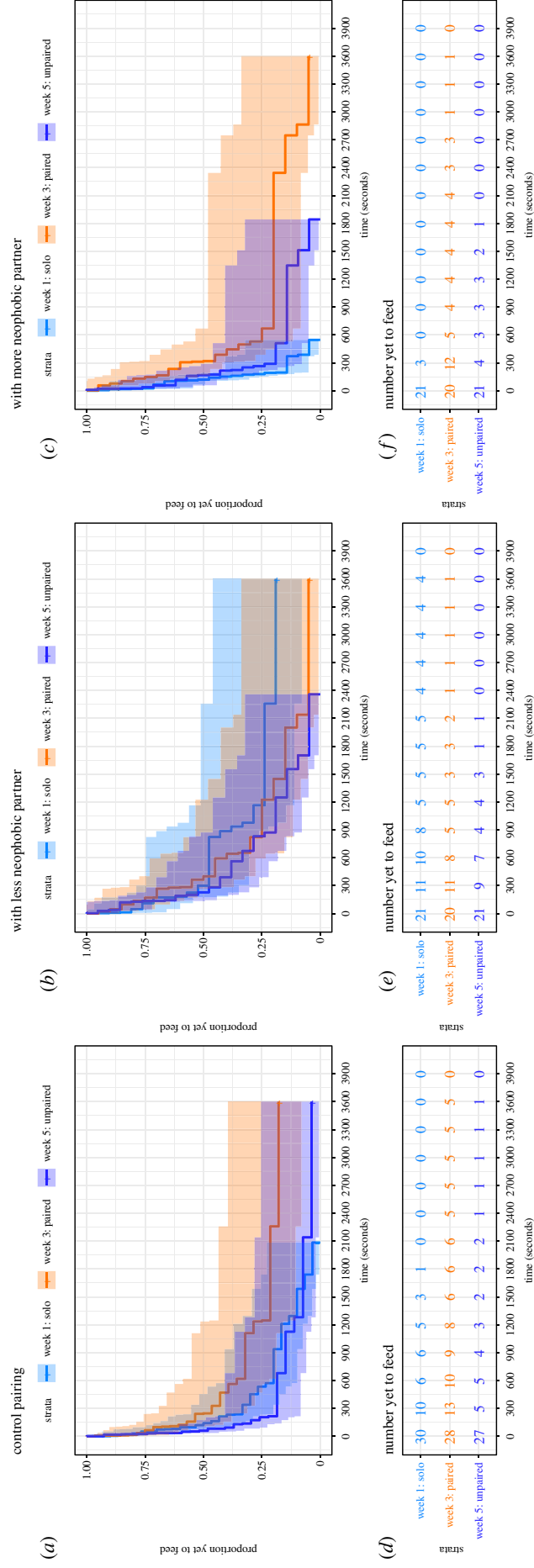


Figure 1. Kaplan–Meier survival curve of house sparrow feeding likelihood after exposure to a novel object, organized by pairing treatment. Curves are split by experiment week and include 95% confidence intervals. In contrast with the first week (solo), being paired with a less neophobic bird increased feeding likelihood after unpairing (week 5) and being paired with a more neophobic bird decreased feeding likelihood while paired (week 3). Models were created using the ‘survival’ package [37] and plots created using the ‘surminer’ package [38].

was also longer than reported in previous work (one week versus up to 3 days; [11]). We can be confident that our results are specific to neophobia because there was no effect of social experience on feeding likelihood during control trials, where no object was presented. Furthermore, feeding likelihood during week 1 and 5 trials did not change in birds with a partner of similar phenotype, confirming that sparrows did not habituate to the experimental procedure. This was important to consider because of the high number of tests and because habituation to neophobia testing has been reported in house sparrows [26]. We highlight these validations because neophobia experiments sometimes lack multiple novel object or control trials, which can make results difficult to interpret [33]. Matched-phenotype pairing indicated a marginal negative effect ($p = 0.07$) of having a cage mate on feeding likelihood in the presence of a novel object (congruent with [13,17,19,21,39] but see [14,16]). This is not an effect of competition to feed because this was not observed during control trials (no object). This behaviour might be explained by both sparrows assessing their partner's behaviour before putting themselves at risk.

Contrary to our predictions, the effects of our social environment on immediate behaviour and long-term social learning varied by behavioural phenotype. This suggests that social conformity may apply to pairs of animals, but that its effects can vary temporally and may depend on phenotype. Being housed with a more neophobic cage mate resulted in a 76% reduced likelihood to feed (95% CI = 47–89% reduction), or on average a 45 min increase in feeding time (range = 28–53 min). However, this effect did not last. While previous studies also reported reduced neophobic behaviour when paired with a less neophobic partner [19,22], we did not find this effect until after house sparrows were separated, which was not tested in previous studies. We offer two potential reasons we did not observe decreased neophobia during pairing. First, house sparrows did not feed on the dish at the same time during the experiment, so more neophobic individuals were naturally slower to feed than their less neophobic partners. Second, a less neophobic sparrow may have been perceived as a better competitor and, as such, the more neophobic individual did not reduce its latency to feed against an individual they were unlikely to outcompete [11]; instead, they decreased neophobia in the competitor's absence.

More neophobic individuals were faster to feed in the presence of a novel object by an average of 166% in solo trials after being unpaired from a bird that approached a

novel object faster than they did. That is, a week after being housed with a less neophobic partner, neophobic house sparrows were on average 2.6 times more likely to feed in the presence of a novel object compared to when initially tested alone. This demonstrates that they (correctly) learned from their partners that novel objects near the food dish were not a threat, though the magnitude of this effect was variable (95% CI = 1.19–5.95%; 0.19–4.9 times more likely to feed). The ability of house sparrows to adjust their behaviour after a social experience is consistent with findings pertaining to food choice [31] and provides evidence of social learning. Furthermore, our study demonstrates that house sparrows can extrapolate information gleaned from the social environment onto new experiences (new objects), unlike the previous study, where sparrows were presented with the same foods as in the social environment [31].

Hormonal or motivational state changes due to the presence of a competitor could be an alternative explanation for the sustained reduction in neophobic behaviour we observed. However, in this case, changes in approach latency should have also been evident in our matched-phenotype controls or no-object control trials. The fact that long-term novel object responses only changed in individuals previously housed with partners with a different behavioural phenotype suggests that social learning indeed occurred. However, the underlying proximate mechanisms mediating this change in neophobia are not known, and, as such, merit further investigation.

Ethics. This work was approved by the Louisiana State University Institutional Animal Care and Use Committee, project 96–2018.

Data accessibility. All the raw data and R Code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.m0cfxpp16> [40].

Authors' contributions. C.R.L. conceived of the study; T.R.K. coordinated the study; T.R.K., K.R.S., C.R.L. carried out fieldwork; T.R.K., M.G.K., K.R.S. participated while C.R.L. led study design; all authors carried out laboratory work; T.R.K. led and C.R.L. assisted data analysis; T.R.K. drafted and M.G.K., K.R.S. and C.R.L. revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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