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Interaction time with conspecifics induces food preference or aversion in the wild Algerian mouse

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ABSTRACT

The social transmission of a novel food preference can avoid unnecessary costs arising from tasting nonedible foods. This type of social learning has been demonstrated in laboratory rats and mice. However, among wild animals, there may be several constraints that make it less effective. Using wild Algerian mice (*Mus spretus*) tested in the laboratory, we demonstrate that a preference for a novel food can be transmitted between Observer and Demonstrator individuals and that it is maintained for at least 30 days. However, only half of the Observers acquired a preference for the same food as the Demonstrators, and only when the duration of oronasal investigation was above a certain threshold ($\geq$122 s); below this threshold ($<$122 s), Observers acquired a preference for the alternative food offered, which was maintained for a shorter time. Sex, size, and identity of individuals did not influence the transmission of social information. The results show that different interaction times will result in animals copying or avoiding the food choices of others. This suggests that the transmission of social information among wild animals is complex and probably influenced by many factors (e.g., dominance, familiarity, and health condition), ultimately conditioning the type of interaction between individuals and its outcome. Testing wild animals and the ecological and social constraints they face is, therefore, an important step in our understanding of how effectively social information is transmitted in nature.

1. Introduction

Social information, the information acquired from the behaviour, physical traits and condition of other individuals (Danchin et al., 2008; Wagner and Danchin, 2010), and the social learning process that follows from it (Heyes, 1994; Hoppitt and Laland, 2008, 2013), can play important roles in the decisions that animals make about their lives. Evidence of social learning has been found in many different taxonomic groups and contexts, for example, when choosing a mate (guppies: Auld and Godin, 2015; fruit flies: Mery et al., 2009), deciding where to live (flycatchers: Doligez et al., 2002), acquiring a novel foraging technique (rats: Aisner and Terkel, 1992; chimpanzees: Whiten et al., 1999; great tits: Aplin et al., 2015), or choosing what to eat (bats: Ratcliffe and Hofstede, 2005; vervet monkeys: van de Waal et al., 2013; bumblebees: Jones et al., 2015). When it comes to deciding what to eat, the role of social information can be especially important. Identifying suitable novel foods or assessing food quality individually through trial-and-error, can be both time and energy consuming (Ratcliffe and Hofstede, 2005, Jones et al., 2015) and it can also be dangerous, as eating the wrong foods can lead to illness (Wilcoxon et al., 1971) or even death (Galef and Clark, 1971; O'Donnell et al., 2010). By acquiring information about the eating habits of conspecifics, animals can more easily learn about novel foods and assess which food items are safe or more nutritious (Hishimura, 2000; Danchin et al., 2004; Kendal et al., 2009).

The best-known studies of social transmission of novel food preferences were done with laboratory rats (*Rattus norvegicus* and *R. rattus*). These studies showed that preference for a novel food was transmitted through oronasal investigation (e.g., sniffing and licking) with a conspecific that had previously eaten the food (Galef and Wigmore,

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1983; Posadas-Andrews and Roper, 1983). The acquired preference was also maintained for at least 30 days after the social interaction (Galef and Whiskin, 2003). Similar experiments have been carried out with the laboratory house mouse (*Mus musculus*) (Valsechi and Galef, 1989; Valsecchi et al., 1996a; Wrenn et al., 2003) and, more recently, with a breeding stock of wild house mice (Forestier et al., 2018), all studies reaching similar conclusions. The molecular, cellular, and neural mechanisms underlying socially transmitted food preferences in mice were also recently unveiled (Munger et al., 2010). Munger et al. described the existence of an olfactory subsystem composed of specialised receptor proteins and sensory neurons for the detection of carbon disulphide (the chemical compound in rodents' breath that is detected during oronasal investigation) and of specialised olfactory bulbs for the association of the carbon disulphide (the social cue) with the food odours (which reach the olfactory bulbs through the canonical olfactory system). The learned association then migrates to the hippocampus, forming long-term food preference memories.

So far, all these studies, and most studies on social learning of novel food preferences in general (for reviews see Galef, 1996; Terkel, 1996), have used laboratory animals. By laboratory animals we refer to subjects that are taken care of, fed and bred by humans, with domestication traits being selected over many generations (Price, 1984; Künzl et al., 2003). These studies have undoubtedly contributed to most of the current knowledge on this subject (Kendal et al., 2010). However, using long-term lineages of laboratory animals can also make the results difficult to generalise (Kendal et al., 2010; Webster and Rutz, 2020), since they may lack ecological agreement. The sex, size and/or identity of the individuals who transmit the information, as they may relate to dominance hierarchies, familiarity levels and personality traits, can represent obstacles or, on the contrary, be facilitators of the transmission process (Valsecchi et al., 1996a; Forestier et al., 2018; Agee et al., 2019), affecting the duration of the social interaction and the learning performance. These are variables that are not as easily accounted for in laboratory studies with domesticated strains, or that are not analysed (Valsecchi et al., 1996b; Rogers-Carter et al., 2018; Belkina et al., 2021). For example, due to years of laboratory rearing, both domestic guinea pigs and laboratory mice are more sociable and less aggressive in comparison with their wild counterparts (Kaiser et al., 2015; Kondrakiewicz et al., 2019). These behavioural phenotypes may facilitate the transmission of information, giving the impression that social learning can be as effective in nature as it is in the laboratory. Studying social learning with wild animal populations, both in the laboratory and in their natural habitats, is thus one of the great challenges ahead. Indeed, the number of social learning studies done with wild animals is increasing (e.g., Valsecchi et al., 1996b; Whiten et al., 1999; Doligez et al., 2002; Solomon et al., 2002; Ratcliffe and Hofstede, 2005; Rymer et al., 2008; Aplin et al., 2015; Forestier et al., 2018; for reviews see Kendal et al., 2010; Galef, 2004; Reader and Biro, 2010) but it is still scarce.

Here, we studied whether preference for a novel food is socially transmitted in a wild population of the Algerian mouse (*Mus spretus*), a Mediterranean endemic species (Mathias et al., 1999). We conducted our study in the laboratory with specimens recently captured from the wild. Our goal was to determine whether, in wild animals, the acquisition of a novel food preference is affected by the quality of social interactions. Namely, we asked whether the sex, size and identity of demonstrator individuals affected the duration of oronasal investigation and, consequently, the learning process. Additionally, we assessed whether the acquired preference was retained for both a short and a long period of time.

Like other rodents, the Algerian mouse relies significantly on its olfactory system to acquire information about its surroundings, food, and conspecifics (Hurst et al., 1996, 1997). Due to its wide distribution and generalist diet, this species is also likely to find new foods frequently, thus having the potential to acquire new food preferences throughout their lives. And because unpalatable and potentially toxic food items can occasionally be found, using social information as part of the species' foraging strategies could be especially important. Likewise, the strong bond observed between mated pairs suggests that individuals often engage in amicable interactions (Cassaing and Isaac, 2007), thereby increasing the likelihood that social learning will occur. This species should, therefore, serve as a good model for studying the transmission of social food preferences in wild specimens. Furthermore, as it is closely related to the house mouse, the same experimental paradigms that have been used for *Mus musculus* (e.g., Valsechi and Galef, 1989) should be easily applied in *Mus spretus*.

Based on finds with laboratory rats (Galef and Wigmore, 1983) and house mice (Valsechi and Galef, 1989), we hypothesised that wild Algerian mice should be able to acquire the food preferences from their conspecifics through social interactions. We, therefore, predicted that appetitive social learning would occur. This means that naive observer individuals must learn to prefer food that has been previously eaten by demonstrator individuals by positively associating the odour of that food (the conditioned stimulus) with the odour of their conspecifics' breaths (carbon disulphide, the unconditioned stimulus). However, we also hypothesise that the learning process can be significantly limited by the quality of social interactions. Therefore, if sex, size, and identity of demonstrator individuals affect the duration of oronasal investigation, social learning may not occur. The quality of social interactions can be affected in such a way that aversive rather than appetitive learning may occur. This would mean that naive observer individuals would learn to reject food that was previously eaten by demonstrator individuals, the odour of which they would negatively associate with the odour of their conspecifics' breaths. This scenario could occur, for example, if observers prefer to avoid the food chosen by dominant conspecifics.

Regarding long-term effects, since some foods consumed by *M. spretus* are seasonal, we predicted that when social learning successfully occurs, it should be relevant enough to be memorised not only for short periods (up to 24 or 48 h), but also for longer periods of time (up to 1 month), similar to findings with laboratory rats (Galef and Whiskin, 2003). Considering that *M. spretus* has a lifespan of 14–15 months (Palomo et al., 2009), 30 days is a considerably long period in an individual's life (c. 4–5 years in human terms). The occurrence of social learning under these circumstances would corroborate its importance in the foraging strategies of this species.

2. Methods

To test the social transmission of novel food preferences in the wild Algerian mouse, we used a modified version of Galef and Wigmore's (1983) and Valsecchi and Galef's (1989) experimental paradigms with laboratory rats and house mice, respectively. We implemented some changes to account for using wild specimens.

2.1. Animal trapping, maintenance and acclimation period

Specimens of *M. spretus* were captured within the Natural Park of Sintra-Cascais, Portugal, between November 2015 and July 2016 using Sherman and wood live traps. Traps were baited with sardine paste and checked every two and a half hours, starting at dusk until 1 am. We captured a total of 60 animals, 37 males (mean weight 13.4 g ± 3.6) and 23 females (mean weight 12.9 g ± 4.5).

Animals were taken to the "Small Mammal Laboratory" at the Faculty of Sciences of the University of Lisbon and maintained under controlled laboratory conditions (20 ± 2 °C; 12 h:12 h light:dark cycle; lights on at 8:00 am). Mice were housed individually in size II Makrolon cages (20.5 ×26.5 ×13.5 cm). Wood shavings were used as bedding, and a cardboard tube, tissue paper and cotton were offered as nesting material and environmental enrichment. Food (maintenance rodent chow in the form of cylindrical pellets, SAFE® A04) and water were provided ad libitum. All animals were weighed at arrival and submitted to an acclimation period of 5–8 days to the laboratory conditions.

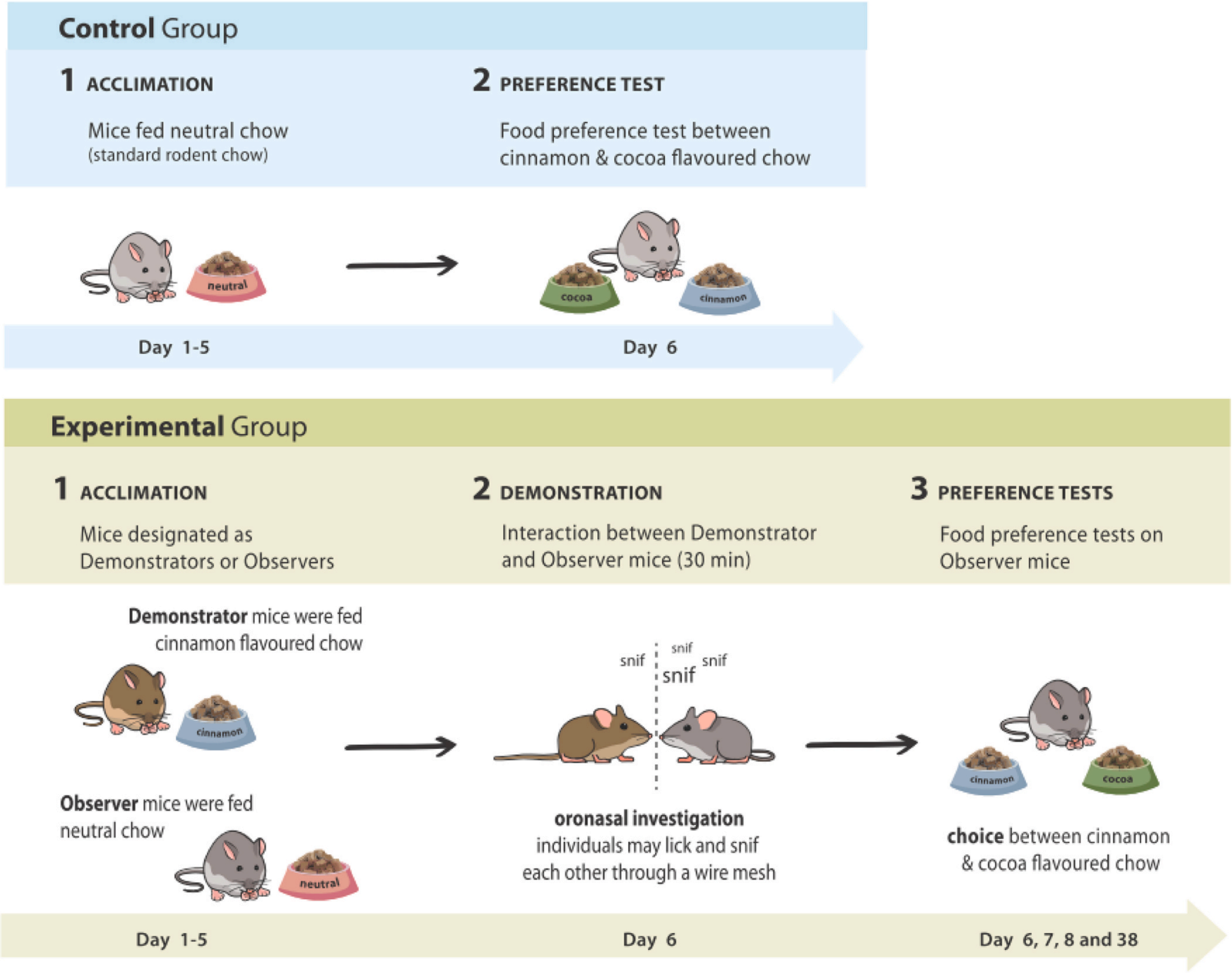

Fig. 1. Experimental procedure. Control mice were fed with Neutral Chow during the acclimation period, after which they were assessed for a spontaneous preference for Cocoa and Cinnamon Chows in a preference test. Mice from the experimental group were designated as Demonstrators or Observers and during the acclimation period they were fed Cinnamon or Neutral Chow, respectively. After acclimation, pairs of Observers and Demonstrators were formed for a 30-min demonstration phase during which Observers could smell cinnamon on the Demonstrators' breaths through oronasal investigation. Then, immediately after the demonstration phase, as well as 24 h, 48 h and 30 days later, preference tests for Cinnamon and Cocoa Chows were performed on Observer mice.

2.2. *Control test*

A control test was performed to determine whether *M. spretus* had a spontaneous preference for any of the experimental foods used: cocoa and cinnamon flavoured rodent chow (Fig. 1). Flavoured foods were prepared by dusting rodent chow (Neutral Chow) with either 2% of cocoa (Cocoa Chow) or 1% of cinnamon powder (Cinnamon Chow) (Galef and Wigmore, 1983). Since both cocoa and cinnamon are brown, both foods had a similarly brown coloration.

During the acclimation period, 24 mice (16 males and 8 females) were first fed with Neutral Chow. Having completed this period, each mouse was tested for its spontaneous food preference. For 1 day, mice received in their cages ≈ 10 g of Cocoa Chow and ≈ 10 g of Cinnamon Chow. Two partitions on the cage feeder kept the food 5 cm apart to avoid flavour contamination. The foods were randomly assigned to either the right or left side of the cage feeder to avoid side bias effects. Subjects and both food types were weighed before (between 10 and 11 am) and after (24 h later) the test. The food preference of each individual was assessed as the proportion of cinnamon preference, calculated as the weight of Cinnamon Chow eaten, divided by the total weight of Cinnamon and Cocoa Chows eaten.

2.3. *Social transmission test*

The social transmission test had three phases (Fig. 1): the acclimation phase, the demonstration (or social interaction) phase and the post-demonstration (or preference test) phase. The animals used in this experiment (experimental group) were not the same as those used in the Control Test.

2.3.1. *Acclimation phase*

In the acclimation phase, animals were assigned randomly to two groups at arrival in the laboratory: Demonstrators ($N = 12$, 5 males and 7 females) and Observers ($N = 24$, 14 males and 10 females). To stage a long-term use of Cinnamon Chow by healthy individuals and ensure their breaths had a strong scent of flavoured Cinnamon Chow during the demonstration phase, Demonstrators were fed with Cinnamon Chow for 5–8 days, while Observers were fed with Neutral Chow. The cinnamon flavouring was added to fresh neutral chow every day to ensure that the odour intensity and amount of flavouring present were similar. The Neutral Chow given to Observers was also replaced every day with a new one.

2.3.2. Demonstration phase

The demonstration phase consisted of staging an interaction between a Demonstrator and an Observer in a glass terrarium (30×40×30 cm) for a 30-min period. Food was absent. A wire mesh placed in the middle of the terrarium prevented mice from direct contact but allowed access to each other's chemical cues through oronasal investigation (e.g., sniffing and licking) (Galef and Wigmore 1989; Valsechi and Galef, 1989). Interactions were staged early in the day (between 9 and 10 am), a period of known high activity in mice, including feeding (Vargas et al., 1987; Gray et al., 1998). This increased the likelihood that the Demonstrators had recently eaten and, consequently, a strong odour stimulus was present in their breaths during the interaction with the Observers. Social interactions were always performed between opposite sex conspecifics, using both females and males as Observers and Demonstrators, as these are the interactions believed to occur most frequently between *M. spretus* in the wild. Males and females are territorial but male territories usually overlap only with those of females (Hurst et al., 1996, 1997). Strong bonding between mated pairs also suggests that both sexes engage frequently in amicable interactions (Cassaing and Isaac, 2007). To keep the number of mice used per experiment to the minimum, each Demonstrator was paired with two different Observers, and each interaction took place on two separate days. All interactions were videotaped and posteriorly analysed to assess the duration and frequency of oronasal investigation between individuals. After the demonstration phase, both Demonstrator and Observer individuals were returned to their home cages; Demonstrators were given Cinnamon Chow ad libitum if they had concluded only one demonstration, and Neutral Chow after they had concluded their second demonstration; Observers initiated the preference test phase (see below). The terrarium and the mesh were washed between demonstrations with detergent and water followed by a 70% ethanol solution and allowed to air dry.

2.3.3. Preference test phase

After returning to their home cages, Observers were tested immediately after the demonstration phase (the within 24 h treatment). For this, they were offered ≈ 10 g of Cocoa Chow and ≈ 10 g of Cinnamon Chow during 24 h. Both foods were available to mice on opposite sides of the food tray as in the Control test. Observers and both flavoured foods were weighed before and after the test, and the proportion of cinnamon preference was calculated as described for the Control test.

Next, to determine if Observers maintained their preference for the novel food over time, Observers were tested in three other time points to evaluate short- and long-term preference: after 24 h, after 48 h and after 1 month. Again, Observers and both flavoured foods were weighed before (between 10 and 11 am) and after (24 h later) the tests. After the 48 h test, individuals were maintained on a diet of Neutral Chow for 30 days. After this period, individuals were again offered ≈ 10 g of Cocoa Chow and ≈ 10 g of Cinnamon Chow and their 1-month preference was evaluated. As for the acclimation phase, the Cocoa and Cinnamon Chows were prepared daily to ensure that the odour intensity and amount of flavouring present were similar.

2.4. Statistical analysis

All statistical analyses were performed with the software R v. 4.2.2 (R Core Team, 2022). Significance was accepted at $\alpha = 0.05$. The response variable was the proportion of cinnamon chow eaten (the weight of cinnamon chow eaten by each individual, divided by the total weight of cinnamon and cocoa chows eaten).

We did three types of analyses. Firstly, we evaluated whether *M. spretus* had a spontaneous (non-random) preference for Cinnamon Chow in the Control group. Secondly, we examined whether the *Duration of Oronasal Investigation* between Demonstrator-Observer dyads, as well as the effects of *Size* (the weight difference between Observers and Demonstrators), *Sex* (the sex of the Demonstrators, which was always the opposite of the sex of the Observers), and identity of Demonstrators (*Demonstrator ID*) influenced the proportion of Cinnamon Chow eaten in the first preference test (the within 24 h treatment). And thirdly, we analysed whether the socially acquired information persisted over time, that is, over the three other time points (*Preference Duration*).

Duration of Oronasal Investigation and *Size* were continuous predictor variables; *Sex* had two groups ("Females"; "Males"); *Demonstrator ID* had 12 groups, as each Demonstrator was tested with two Observers; and *Preference Duration* had four groups ("Within 24 h", "After 24 h", "After 48 h", and "After 1 month").

For the comparison of the Control group with random choice (i.e., with a 0.5 proportion of Cinnamon Chow eaten), we used a one-sample t-test. For the analyses of the preference test within the 24 h time point, we applied Generalized Linear Models (GLMs) with the R package betareg, as the beta regression is the most appropriate for when the response variable is a proportion (Cribari-Neto and Zeileis, 2010). Because the proportion of Cinnamon Chow eaten varied continuously between 0 and 1 (as required by betareg), but sometimes assumed the extreme values of 0 and 1, we transformed the data using the formula (y (n − 1) + 0.5)/n where *n* is the sample size (Smithson and Verkuilen, 2006). To obtain the models output, we used the *joint_tests* function from the R package emmeans (Lenth et al., 2020). For pairwise comparisons between treatments, when needed, we used the *emmeans* function from the same package. For comparisons with random choice, we used one-sample t-tests. For the analysis of *Preference Duration*, we applied the beta regression again, but with a Generalized Linear Mixed Model (GLMM) from the R package glmmTMB (Brooks et al., 2017). The GLMM was needed in this case to account for the repeated measures, since we used data from the same Observer mice in 4 time points. Again, for comparisons with random choice, we used one-sample t-tests.

3. Results

3.1. There was no spontaneous preference for the novel food

The proportion of Cinnamon Chow eaten by control individuals ($N = 24$) was not significantly different from randomness. Naive mice did not eat significantly more Cinnamon than Cocoa flavoured Chow (one-sample t-test: $t = -0.71873$, d.f. = 23, $p = 0.4795$; mean = 0.4533).

3.2. The learned preference for the novel food increased with the duration of oronasal investigation

The proportion of Cinnamon Chow eaten was not significantly influenced by *Sex* (GLM with beta regression: F-ratio = 2.741, d.f. = 1, $p = 0.0978$), *Size* (GLM with beta regression: F-ratio = 3.385, d.f. = 1, $p = 0.0658$), nor by the *Demonstrator ID* (GLM with beta regression: F-ratio = 1.302, d.f. = 11, $p = 0.2159$). The proportion of Cinnamon Chow eaten was only influenced by the *Duration of Oronasal Investigation* (GLM with beta regression: F-ratio = 66.832, d.f. = 1, $p < 0.0001$): the range was 9 s to 408 s of oronasal investigation, and the higher the total interaction time with conspecifics, the higher the proportion of novel food eaten by Observers (Fig. 2a).

Only half of the individuals learned to prefer Cinnamon Chow, meaning that the duration of oronasal investigation revealed two natural groups of individuals (quasi-experimental design, Cook, 2015) – those that interacted less than 122 s and rejected Cinnamon Chow (aversive learning) and those that interacted 122 s or more and preferred Cinnamon Chow (appetitive learning). We, therefore, repeated the analysis with the variable *Duration of Oronasal Investigation* categorised into these two groups. Our goal was to verify whether they were significantly different from each other and from the control group, and whether their acquired preference was significantly different from randomness.

We found a significant difference among the three groups (GLM with beta regression: F-ratio = 16.406, d.f. = 2, $p < 0.0001$). The two groups

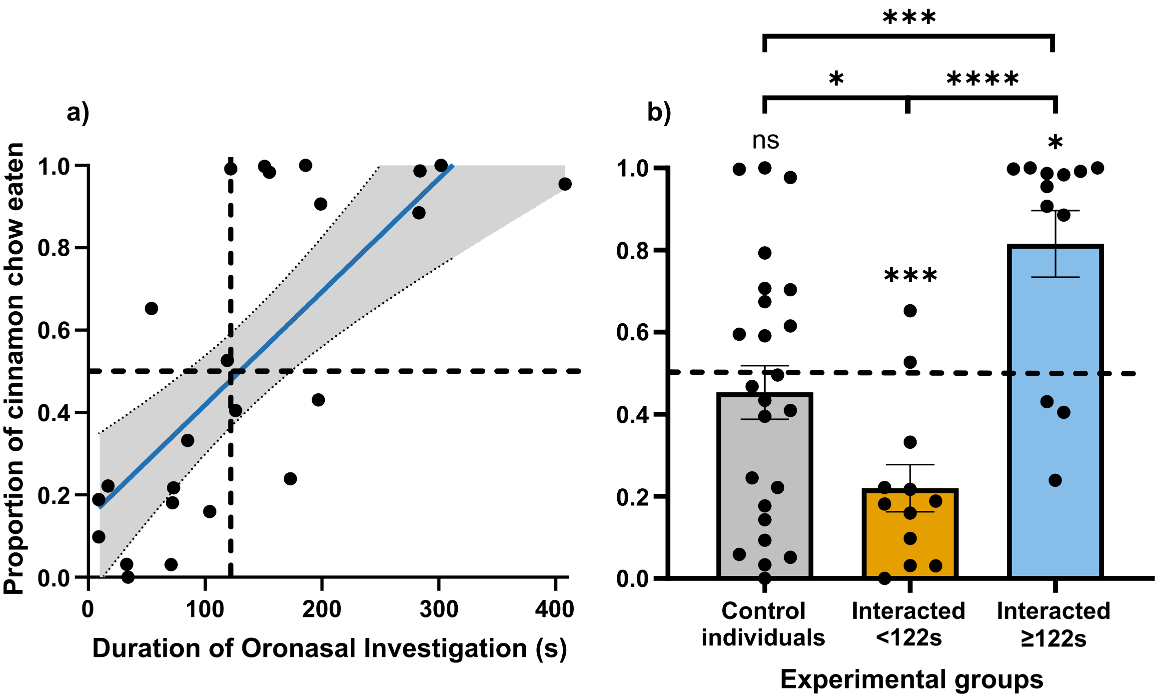

Fig. 2. The learned preference for the novel food increased with the duration of oronasal investigation. (a) Scatter plot of the proportion of Cinnamon Chow eaten by Observer individuals ($N = 24$) over the interaction time. The straight blue line corresponds to the regression fit. The grey area represents the confidence bounds for the regression line. Each black dot represents an individual. The horizontal dashed line represents random choice. The vertical dashed line represents the 122 s boundary. From this time point onwards, most mice started to prefer cinnamon highly above randomness. (b) Bar plots of the proportion of Cinnamon Chow eaten by Control mice (the gray bar) and two groups of Observer mice, those that interacted less than 122 s with conspecifics (the orange bar) and those that interacted 122 s or more (the blue bar). Each black represents an individual. The horizontal dashed line represents random choice. Asterisks above bars indicate comparisons with random choice (ns = non-significant difference). Horizontal solid lines indicate pairwise comparisons between groups. * $p < 0.05$; *** $p < 0.001$; **** $p < 0.0001$.

of Observer individuals were significantly different from the control group (pairwise difference between the control group and the <122 s group: z-ratio = 2.145, $p = 0.0320$; pairwise difference between the Control group and the ≥122 s group: z-ratio = −3.923, $p = 0.0001$). The two groups of Observer individuals were also significantly different from each other (pairwise difference between the <122 s group and ≥122 s group: z-ratio = −5.553, $p < 0.0001$). The preference for Cinnamon Chow of the ≥ 122 s group was significantly greater than that expected by chance (one-sample t-test: $t = 3.8787$, d.f. = 11, $p = 0.0026$; mean = 0.8152). On the other hand, the proportion of Cinnamon Chow eaten by the < 122 s group was significantly below randomness (one-sample t-test: $t = -4.8795$, d.f. = 11, $p = 0.0005$; mean = 0.22) (Fig. 2b).

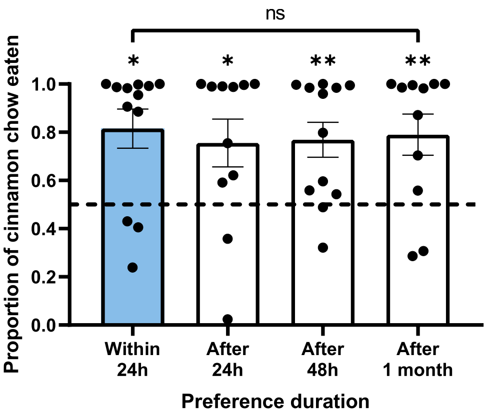

Fig. 3. The learned preference for the novel food by Observers that learned appetitively persisted over time. Bar plots of the proportion of Cinnamon Chow eaten by Observer mice that interacted 122 s or more with a Demonstrator over 4 time points. The blue bar shows the same data as the blue bar in Fig. 2b. Each black dot represents an individual. The horizontal dashed line represents random choice. Asterisks above bars indicate comparisons with random choice. The horizontal solid line indicates the group level comparison. ns = non-significant difference, * $p < 0.05$, ** $p < 0.01$.

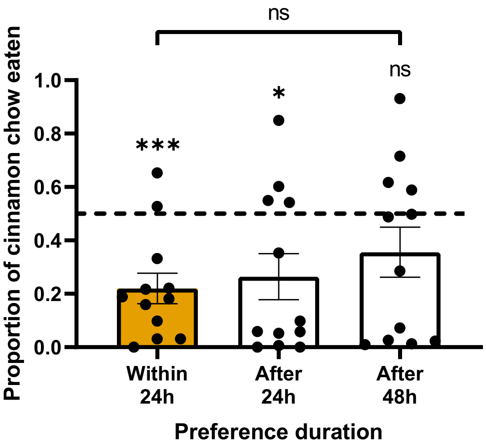

Fig. 4. The learned preference for the novel food by Observers that learned aversively did not persist over time. Bar plots of the proportion of Cinnamon Chow eaten by Observer mice that interacted less than 122 s with a Demonstrator over 3 time points. The orange bar shows the same data as the orange bar in Fig. 2b. Each black dot represents an individual. The horizontal dashed line represents random choice. Asterisks above bars indicate comparisons with random choice. The horizontal solid line indicates the group level comparison. ns = non-significant difference, * $p < 0.05$; *** $p < 0.001$.

3.3. *The learned preference for the novel food by Observers that learned appetitively persisted over time*

The proportion of Cinnamon Chow eaten did not significantly vary over time (GLMM with beta regression: $\chi^2 = 0.841$, d.f. = 3, p = 0.8396), and persisted above randomness. The preference for Cinnamon Chow was significantly above randomness within 24 h (as also seen in Fig. 2b, the blue bar), after 24 h (one-sample t-test: t = 2.5805, d.f. = 10, p = 0.0274; mean = 0.7557), after 48 h (one-sample t-test: t = 3.7154, d.f. = 11, p = 0.0034; mean = 0.7687), and after 1 month (one-sample t-test: t = 3.3907, df = 10, p = 0.0069; mean = 0.79) (Fig. 3).

We removed one outlier from each of the treatments "after 24 h" and "after 1 month" with the R package "rstatix", using the percentiles' method (Kassambara, 2022). Outliers do not correspond to the same individual in both treatments. With the outliers, the preference for Cinnamon Chow was only marginally significantly above randomness in both cases: after 24 h (one-sample t-test: t = 1.7831, d.f. = 11, p = 0.1022; mean = 0.6946; preference for Cinnamon Chow by the outlier = 0.02); and after 1 month (one-sample t-test: t = 2.1948, df = 11, p = 0.0505; mean = 0.7241; preference for Cinnamon Chow by the outlier = 0.00).

3.4. *The learned preference for the novel food by Observers that learned aversively did not persist over time*

The proportion of Cinnamon Chow eaten by Observers that learned aversively did not significantly vary over time (GLMM with beta regression: $\chi^2 = 0.8262$, d.f. = 2, p = 0.6616). It was significantly below randomness within 24 h (as also seen in Fig. 2b, the orange bar), and after 24 h (one-sample t-test: t = −2.7284, d.f. = 11, p = 0.0196; mean = 0.2641), but not after 48 h (one-sample t-test: t = −1.5393, d.f. = 11, p = 0.152; mean = 0.3556). Because of that, we did not test the 1-month preference of these individuals (Fig. 4). We removed two outliers from the "after 48 h" treatment and the results did not change (one-sample t-test: t = −1.8893, d.f. = 9, p = 0.0914; mean = 0.3326; preference for Cinnamon Chow by the outliers = 0.0094 and 0.9309).

4. Discussion

Transmission of social information should be favoured when stimuli are new, or their current quality is difficult to assess (Wagner and Danchin, 2010; Danchin et al., 2004; Valone and Templeton, 2002; Laland, 2004). In the context of foraging, when faced with novel foods, naive individuals can decide whether to eat it or not based on the choices of experienced conspecifics (Galef and Wigmore, 1983; Posadas-Andrews and Roper, 1983; Galef and Whiskin, 2003; Valsechi and Galef, 1989; Galef, 1996; Terkel, 1996; Hishimura, 2000). While this has been shown to occur in several species of laboratory rodents, here we ask whether it is also the case for a wild rodent species when under laboratory-controlled conditions. In particular, we asked if social information is efficiently transmitted and sufficiently relevant to persist over time in wild individuals of the Algerian mouse (*Mus spretus*). We examined the effects of size, sex and identity of demonstrator individuals, as well as of the duration of oronasal investigation (e.g., sniffing and licking) on the success of social transmission of novel food preferences.

Our results show that transmission of social information can occur in the wild Algerian mouse. This species has a generalist diet, feeding mostly on grass seeds, plants and insect larvae (Palomo et al., 2009). Wild individuals are thus probably predisposed to try novel foods and, by this, should occasionally eat unpalatable and potentially toxic food items. Hence, the use of social information as part of the species' foraging strategies may be especially important. Our results show that, similarly to laboratory rats (Galef and Wigmore, 1983) and house mice (Valsechi and Galef, 1989), wild Algerian mice are also able to acquire a food preference from their conspecifics through social interactions, confirming that this behaviour can be generalizable from long-term lineages of laboratory animals to animals born in the wild.

However, we also found that the effectiveness of social information among wild Algerian mice depends on the duration of oronasal investigation, and that only when the duration is above a certain threshold, does social learning persist over time. In more detail, our results show that in the absence of social information, naive individuals did not have a spontaneous preference for any of the novel foods tested (Cinnamon and Cocoa flavoured Chow), but when in the presence of social information, about half of the individuals acquired a food preference for the same food eaten by their conspecifics. If oronasal investigation between Observers and Demonstrators was longer than 122 s, Observers acquired a similar food preference to that of Demonstrators (Cinnamon Chow), a preference that persisted for at least a month. On the contrary, when the duration of the interaction was short (< 122 s), Observers ate a higher proportion of the alternative chow offered (i.e., Cocoa Chow), and this preference did not last more than 24 h.

To our knowledge, the duration of oronasal investigation between Observers and Demonstrators has never been considered in wild rodents. In studies with laboratory house mice and rats, individuals are allowed to interact for a fixed period (usually 30 min) but the duration of oronasal investigation over that period is rarely accounted for or does not influence the transmission of information (Awazu and Fujita, 2000). Nevertheless, in a more recent study, a shorter 15-min interaction period failed to elicit a food preference in Observer rats (Agee and Monfils, 2018). Although the duration of oronasal investigation was not measured, a shorter interaction period probably compromised the total time the rats could spend in oronasal investigation and, therefore, may have hindered the transmission of social information.

In our case, however, short times of oronasal investigation did not prevent the transmission of information. Individuals in this condition were able to detect the odour of the novel food in the Demonstrator's breath because they were able to avoid it later. Therefore, short times of oronasal investigation are probably a reflection of a negative interaction between Observer-Demonstrator dyads (aversive learning). The difficulty is in knowing what caused these negative interactions.

For instance, subordinate male rats (Awazu and Fujita, 2000) were suggested as being more effective in transmitting social information about food than dominant individuals (but see Monfils and Agee, 2019, Fulenwider et al., 2021 regarding methodological issues). Subordinate male rats also seem to evade competition, by avoiding consuming the same food as dominant same-sex individuals and eating an alternative less favoured food (Smith et al., 1991). In our study we used male-female pairs of individuals as Observer-Demonstrator dyads. Because males, or larger individuals, are generally more dominant than females, or smaller individuals, we could have expected female or smaller demonstrators to be better at transmitting food preferences. However, we did not find significant sex or size effects of demonstrator individuals. The personality of both Demonstrators and Observers may also have influenced the transmission of social information, affecting, for example, the willingness to interact with each other during the demonstration phase and, hence, the duration of oronasal investigation. However, recent work in mice by Damphousse et al. (2019) does not appear to support this hypothesis: personality (boldness and sociability) did not affect the strength of the acquired preference. If the same applies to *M. spretus*, then personality is unlikely to have affected preference acquisition.

Thereby, a better explanation for the negative interactions could be the health status of individuals. Rodents are renowned for their ability to gather an array of information about their conspecifics solely based on chemical cues, for instance, dominance, sex and kinship but also health condition (Novotny et al., 1990; Kavaliers et al., 2005, 2006; Asaba et al., 2014; Ferkin, 2018). House mice are known to avoid conspecifics that are sick (acute inflammatory state, Boillat et al., 2015) or parasitised (Kavaliers et al., 2006) on the basis of chemical cues alone. While not so much is known on the type of information that is conveyed through chemical cues in the Algerian mouse (Hurst et al., 1994, 1996), it is reasonable to expect that, similarly to the house mouse, *M. spretus* is also able to obtain information from their conspecificś health condition. We hypothesise that if Observers were paired with more parasitised (Kavaliers et al., 2006) or stressed (Savignac et al., 2011) Demonstrators, these cues could have led Observers to have an aversive reaction to Demonstrators, engage less time on oronasal investigation with them, and reject the food eaten by these individuals. However, there was no influence of the Demonstrator on the outcome of the interaction. If some were more stressed or parasitised than others, Observers paired with the same Demonstrator should have had the same learning performance, which was not the case. This suggests that the nature of the interaction (positive or negative), leading to the preference or rejection of cinnamon, depended on both individuals. The familiarity between Observer and Demonstrator may be one such factor.

Contrary to laboratory house mouse and rat studies (Galef and Wigmore, 1983; Valsechi and Galef, 1989), subjects in our experiment were not allowed to familiarise with each other before the social interaction – which we avoided to prevent individuals from establishing relationships that could influence the interaction phase of the experiment, as is known to occur in rats (Galef and Whiskin, 2003; Agee et al., 2019) and house mice (Forestier et al., 2018). While this allowed the elimination of potential variation, it may have affected social interactions. Furthermore, the use of wild animals implies that familiarity and kinship relations between individuals are also unknown. Therefore, any effects these may have in the interactions between individuals are unaccounted for in our study. However, evidence on the effects of familiarity and kinship are not consistent between species. Studies in laboratory rats indicate that unfamiliarity in the context of socially transmitted food preferences leads to a higher interaction time (Galef and Whiskin, 2003; Agee et al., 2019) but does not influence the duration of oronasal investigation, nor does it significantly influence the proportion of demonstrator's food eaten (Agee et al., 2019; Awazu and Fujita, 2000). On the contrary, in the Mongolian gerbil (*Meriones unguiculatus*), familiarity between individuals influences the observer's preference: observers failed to acquire a preference when demonstrators were unfamiliar but not when they were kin or familiar (Valsecchi et al., 1996a). The same was found in female house mice of wild origin (*Mus musculus domesticus*) (Forestier et al., 2018). Whether unfamiliarity led to a decrease in the duration of the interactions in *M. spretus* – caused by a more cautious attitude towards unfamiliar individuals, or to an increase – driven by curiosity about a novel individual, is something we do not know, and its inconsistency among species makes it difficult to extrapolate.

Independently of the specific role that dominance, personality, health, or familiarity may play, our findings suggest that in wild *M. spretus*, the dynamics of social interactions can be quite complex and seem to pose significant constraints to the information transmission process (Valsecchi et al., 1996a; Choleris et al., 1997; Forestier et al., 2018; Agee et al., 2019).

Equally important to understanding how social transmission of food preferences occurs in wild animals, is whether the acquired preference is maintained over time (Galef and Whiskin, 2003). Our results show that preference for the Observer's food persisted over short (24 h) and medium-term (48 h) periods, as well as over a long period (1 month) without further contact with the food. Considering the generalist feeding habits of *M. spretus* (Palomo et al., 2009), it is likely that they feed on many different food types over their lifetime. As such, remembering which of these are safe and nutritious, should be advantageous, allowing individuals to forage more safely and efficiently. However, a recent study in rats suggests that maintaining the preference for such a long time may be an artifact of the experimental protocol. When allowed to forage with other individuals, irrespective of whether they had the same or a different food preference, rats tended to lose their preference for the novel food (Damphousse et al., 2019). On the contrary, individuals that foraged in isolation maintained their preference for at least 20 days. Future studies may clarify whether the same also occurs in *M. spretus*.

Interestingly, we also find that when Observer individuals rejected the food preferred by Demonstrators, the aversive preference did not persist after 24 h, suggesting that learning to reject is not as effective as learning to prefer. This may have been the result of a less consolidated memory due to the short interaction time, or the result of cognitive plasticity, as these Observers may have realised that the social information that made them reject cinnamon was outdated after three days of exposure to the food with no consequences, namely health problems, as discussed above. The literature suggests, in fact, that forgetting can be an adaptive strategy (Kraemer and Golding, 1997) and that aversive learning tends to be forgotten more quickly (Brea et al., 2014). This is so because the optimal strategy, at least theoretically, is to update the valence of previously learned information, especially when the initial conditioning was aversive, because a resource that is no longer aversive can start to be used (Brea et al., 2014).

We limited this study to male-female interactions. In *Mus spretus*, male territories overlap female territories, but not the territories of other males (Hurst et al., 1996, 1997), so male-female dyads are likely the most common for this species and, thus, the most socially relevant. Future studies could investigate the social transmission of food preferences with other dyad combinations to understand whether the transmission of information between same-sex dyads is equally effective. However, as most studies in rodents have been done with same-sex dyads, and generally with males only (e.g., Agee and Monfils, 2018), and we found results similar to those studies, it is likely that *M. spretus* dyads of the same sex will also give similar results.

Another potential limitation of our study is that we kept Demonstrators and Observers separated by a wire mesh. It prevented mice from direct contact but allowed access to each other's chemical cues through oronasal investigation (Galef and Wigmore 1989; Valsechi and Galef, 1989). Direct contact could have triggered aggressive dominance behaviours, or sexual interactions that could have diverted the animals' attention from oronasal contact and the transmission of food preferences. However, more recent studies no longer use this barrier (e.g., Agee and Monfils, 2018), despite using lab-reared animals and same-sex dyads. Even so, it would be interesting to redo these experiments without the wire mesh to see if free interactions between wild Algerian mice and male-female dyads improves or worsens social learning.

We only tested social transmission of food preferences for one food flavour (cinnamon) and not for both (cinnamon and cocoa). A control test was performed to determine whether *M. spretus* had a spontaneous preference for any of the flavours and we found they did not. So, training all the Demonstrators with cinnamon, instead of half with cinnamon and half with cocoa, also allowed to test if after the demonstration phase observers' preference for cinnamon deviated from random choice. This strategy has been followed by some recent studies (e.g., Agee et al., 2019) and helped us reduce the number of animals that had to be captured in the wild and thus disturb the natural populations as little as possible. Nevertheless, we recognise that training groups of demonstrators for each flavour is an additional control and helps generalise the findings for more than one type of food.

Despite these limitations, having tested the social transmission of food preferences in wild animals was an important step in our understanding of the role of social learning in nature, namely of the different behavioural outcomes that may arise from it. Mainly, our results show that interaction time with conspecifics is crucial for the social transmission of food preferences among wild animals. We found that only half of the individuals learned to prefer the same food as conspecifics, revealing two natural groups of individuals (quasi-experimental design, Cook, 2015), this being a result that has never emerged from studies with laboratory animals. We do not know what caused this dichotomy, but it may have resulted from various social factors, such as dominance relationships, familiarity, or the health condition of conspecifics, which are generally less prevalent factors in laboratorial animals. These differences in interaction time between wild animals can lead to lasting food preferences or, on the contrary, to less lasting aversive learning. Both will have different consequences for the direction and stability of social information transmission chains in nature and the process of cultural evolution. This social learning duality can also be especially important for generalist species, like the Algerian mouse, particularly when exploring a new environment with new types of food. The occupation of wild habitats by man is ever-growing. Urban environments can offer abundant, albeit novel, food resources. To thrive in such environments, individuals must learn to recognise these resources. Social learning in such circumstances, both in its appetitive and aversive components, may allow individuals to adjust more quickly and take advantage of the best foods available.

Ethics Statement

After the Long-Term Preference test, all animals were released back into the wild in the locations where they were captured. This project was carried out considering the ethical guidelines stated in the "Guidelines for the treatment of animals in behavioural research and teaching" (Association for the Study of Animal Behaviour and Animal Behaviour Society, 2020) and authorised by the relevant Portuguese competent authorities, ICNF (license number 528/2016/CAPT) and ORBEA (Statement 2/2017).

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CRediT authorship contribution statement

R.S.A., A.M.C. and S.A.M.V. designed the research and wrote the manuscript. R.S.A. and A.M.C. conducted the fieldwork and collected field and laboratory data. R.S.A. and S.A.M.V. analysed the data. M.L.M. revised the manuscript. All authors gave final approval for publication.

Competing interests

The authors declare no competing interests.

Data Availability

Data is provided as supporting material.

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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.2023.104927.

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