Evidence for social learning in a granivorous passerine bird, and for its independence from personality

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ABSTRACT

Individual learning is a way that animals use to adaptively adjust their behaviour to conditions taking advantage of previous experiences. However, individual learning includes risks and costs that can be overcome by learning from others. Thus, several social and gregarious species, across many taxa, rely on social learning. Despite its relevance, the ability to learn from observation of others behaviour was tested in only a few species of birds. It is particularly interesting to test this capability in granivorous gregarious species, because they likely follow environmental cues to forage. We conducted a series of tests on social learning in a foraging task with a small cardueline finch, the Serin (*Serinus serinus*). We used an observer-demonstrator paradigm where observers were given the opportunity to learn to reach hidden food from observation of demonstrators that were previously trained to perform the task. Almost half of the birds tested were capable of learning (40%) from a conspecific in a colour-food association experiment, and learners were able to remember the association after fifteen days. Also, almost half of the birds tested for this revealed to be capable of reversal learning. The ability to learn was not influenced by sex or age, of both demonstrators and learners. However, learners had longer wings than non-learners. Perhaps, individuals proficient in social learning have a foraging efficiency advantage so that they can invest more energy in feather growth. We wondered what could explain the ability of learning by some but not all. Thus, we tested the birds for personality differences. Although we found repeatable personality traits using the novel object and mirror personality tests, they did not explain the differences in learning ability.

Keywords: Boldness, Memory, Personality, *Serinus serinus*, Sociability, Social learning

INTODUCTION

Learning through personal experience is a fundamental process of interacting with the environment, it is widespread in animals (LeDoux 2023 – The four realms of existence; Harvard University Press. Cambridge Mass.) and is essential to survive especially in an ever-changing environment. The ability to learn from others is a more specific form of learning, far more complex but with a number of advantages (Laland, 2004). In fact, asocial learning exposes individuals to the threat of direct interaction with the environment and its dangers (Kendal *et al.*, 2009). This can largely be avoided through social learning (Heyes, 1994), a case in which individuals can benefit from the experience of others, typically conspecifics. In the last few decades many studies on social learning have broadened our understanding of this behaviour in an increasing number of animals with different social lifestyles. This goes from social species, such as meerkats (Thornton & Malapert, 2009), to gregarious ones like starlings (Templeton and Giraldeau, 1996), and even solitary species, such as the common octopus (Fiorito and Scotto, 1992) and in insects such as Drosophila (Mery *et al.*, 2009). Song learning in birds is a well-known and thoroughly studied case of social learning, where young birds need to learn from the adult's performance (Brenowitz & Beecher, 2005; Hultsch & Todt, 2004). It is a special case of social learning, subject to extreme selection that conducted to a genetically channelled developmental process (Brainard & Doupe 2002, Nature; Scharff & White, 2004), that controls when and what type of information the animals can learn, and we will not deal with it here. As a shortcut to acquire valuable knowledge, social learning appears to be always adaptive but, actually, mindless copying is not an effective strategy. As predicted from theoretical models and observed in nature, animals do not rely solely on indiscriminate social learning (Kameda & Nakanishi, 2002). Instead, natural selection has favoured the establishment of several "social learning strategies" (Laland 2004; Kendal *et al.,* 2005; Kendal *et al.,* 2009). For instances, social learning is preferred when asocial learning is costly or when personal information is not updated to the current situation, exemplified in nine-spined sticklebacks and worker honeybees (Van Bergen *et al.,* 2004; H Grüter's et al., 2010; Grüter & Ratnieks, 2011). Also important is to learn from a successful individual instead of a subordinate one (Greene, 1987), or to copy the majority (Pike & Laland, 2010).

Learning relies on memory in order to benefit from the useful information gathered. In an ever-changing environment, it is essential to adapt previous knowledge to novel circumstances. In some cases, it requires to abandon an association established and replace it by a new one. This cognitive ability can be discerned in tests of reversal learning. Variations of this test have been explored to great success on a variety of mammals, such as rats, macaques, and pigs, (Guillamón et al. 1986; Ha et al. 2011; Roelofs et al. 2017), and also birds, such as corvids and great tits (Cauchoix et al., 2017; Bond et al., 2007). In many cases, individuals were able to learn an associative rule and then, after being exposed to a situation where the rule was reversed, they were capable of adapting their behaviour to the new conditions. Some evidence suggests that in guppies and other vertebrates, females are faster and more precise at reversal learning than males (Petrazzini et al., 2017; Guillamón et al. 1986; Ha et al. 2011; Roelofs et al. 2017).

In many species, individuals have been observed to consistently show a preference between personal or social information (e.g. Dubois et al., 2012; Hämäläinen, 2017; Rendell et al., 2011; Rosa et al., 2012). This individual variation in social learning reliance might be related to some individual's characteristics, such as sex (Rendell et al., 2011; Rosa et al., 2012), age (Thornton & Malapert, 2009) and even personality (e.g. Kurvers et al., 2010; Marchetti & Drent, 2000;

Nomakuchi, Park, & Bell, 2009). Biologists now define the latter as an individual behavioural difference that is consistent over time and across different contexts (Rèale *et al.*, 2010). Thus, such behavioural differences might impose constraints and affect the cost/benefit trade-offs associated with personal and social information use. Although a recent review on the interaction between cognition and personality found evidence for a small but significant relationship (Dougherty and Guillette, 2018), its direction is highly variable, meaning that across the analysed species personality appears to affect cognition in different ways. This finding does not align with the prior favoured hypothesis that considers, "proactive", bold/explorative, animals capable of experiencing more of their environment, more quickly, thus encountering to-be-learned associations more readily than "reactive", shy/less explorative, individuals (Sih and Del Giudice, 2012).

In the case of social learning, its association with personality is also not clear cut. Studies performed on great tits and sticklebacks have shown that fast exploring individuals make more, and faster use of social information gained from observing demonstrators (Marchetti & Drent, 2000; Nomakuchi *et al.,* 2009). However, a subsequent study also with great tits found the opposite, in that slow explorers based their behaviour on prior knowledge of both personal and social origin more than fast explorers, who tended to act less according to available information (Smit & van Oers, 2019). Other findings where bolder individuals prefer to ignore or even avoid conspecifics were reported for guppies (Trompf & Brown, 2014) and barnacle geese (*Branta leucopsis*) (Kurvers *et al.*, 2010), while in other species bolder individuals are more proficient social learners, such as chacma baboons (*Papio ursinus*) (Carter *et al.* 2014).

Birds benefit from social learning in many different contexts such as migration routes, predators' recognition, mate choice and foraging to name a few (Slagsvold and Wiebe, 2011). While it is known that group living birds that practice active hunting, such as great tits and marsh harriers, are capable social learners (Aplin et al., 2013; 2015; Kitowski, 2009), less is known about granivorous birds, which do not have to search for prey and may not benefit as much from observing others. Thus, our main question was: do animals that feed on more readily available food rely on social learning? The objective of the present study is to investigate social learning in a bird belonging to an underrepresented group of avian species in literature, the granivorous and gregarious passerines. In the serin (*Serinus serinus*), individuals gather in flocks for most of the time, forming particularly large ones during the winter season, where social learning could be beneficial during foraging. Following previous findings on gregarious species of birds, we expected that social learning would vary among individuals, with just part of them revealing the ability to learn fast (Aplin et al., 2013; 2015; Kurvers et al., 2010). In addition, we hypothesised that traits such as the age and sex of the observers might have a role in the social learning capabilities of the birds. We set a two-action and control experimental design that involves observers and demonstrators to test if serins are capable of and reliant on social learning and if it is dependent on sex, age, or physical characteristics. We also wanted to further investigate the learning skills of these birds by testing their retention memory and the ability for reversal learning. Finally, considering the existence of individual differences in social learning, we investigated whether differences in personality could explain them. We expected more sociable observers to be more attentive of the demonstrator performance and thus increasing their chance of social learning. Bolder individuals were expected to interact more easily with the foraging board giving them the possibility to perform the observed behaviour from the beginning, without being driven away from novelty.

Materials & Methods

Subjects and housing

Wild serins were captured in 2021 and 2023, in rural areas around Coimbra (Portugal). All 47 adults captured were transported to the aviary of the University of Coimbra, where they were housed by sex in cages,100 x 50 x 50 cm in size, holding a maximum of four individuals and kept under natural light. Cages were provided with water and food containing a standard mix of seeds for passerines birds, with supplementation that was provided as adequate. The testing room was mostly illuminated with artificial light emitting a light spectrum similar to sunlight. All testing sessions were filmed with two cameras, one framing the whole testing area and one zooming into the testing apparatus. Filming and behavioural scoring were made using the software Observer XT 10. All birds were ringed with plastic black numbered rings (AvianID), and several measurements were collected from each individual: age, weight, left and right wing length, tarsus length, beak length, beak width, beak height and ecto-parasite load (Annex 1). Age classes only considered two categories, first year and older birds, and was based on the moulting of the coverts wing feathers (Svensson, 1992). Morphometric variables were normally distributed (Shapiro-Wilkins test). A Principal Components Analysis (PCA) was performed to reduce the seven morphometric variables into two Principal Components that explained 60% of the variance. PC1 had positive loading on wing length (Annex 1), while PC2 had positive loading on the height and width of the beak and negative on beak length. The birds were released in their capture sites by the end of the study.

Colour-food association task

The social learning test consisted of a foraging task in which birds were rewarded with hidden food when they displaced the disks of a specific colours. A random group of birds was assigned to a demonstrator role. Demonstrators were trained to learn a food-colour association through a gradual learning process. During the testing phase the observers had the opportunity to learn from the observation of the demonstrators' behaviour. The food-colour association task was constituted of a wooden board (Fig. 1) with sixteen wells arranged in a 4x4 matrix. During tests half of the wells were covered with plastic disks of two colours: four red and four blue. Disk colours were chosen for high contrast and for not being part of the birds' colouration. Food was only available in the wells covered with the colour the demonstrators were trained with. Both during training of demonstrators and the trials of the observers, the disposition of the colour disks in the wells was randomized for each trial applying random permutations generated in R v.4.3.1 (R Core Team, 2023). A small amount of seeds was placed in the wells covered by the disks of the association colour, and remained consistent across all trials with the same bird. In order to have access to the food, the birds had to displace the disks of the right colour. The randomization of disks location prevented any possible association between food and position. After each trial, the disks and the board were washed to exclude any possible olfactory cues.

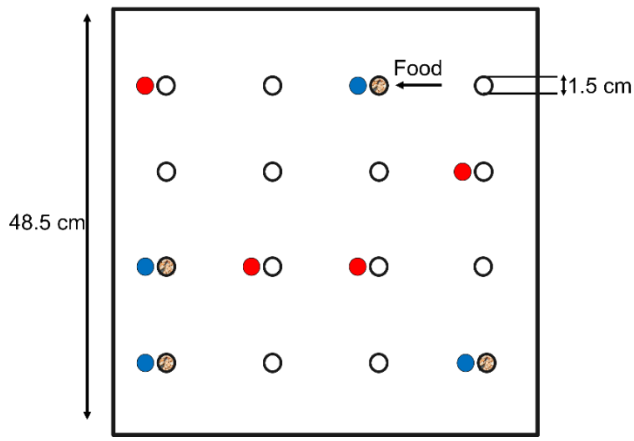

Figure 1: *Graphical representation of the foraging task. The square represents a wooden board with sixteen equally distant wells carved on the top side. Eight disks of two colours are placed in correspondence of the wells with a random disposition in each trial. For each bird food is present in the wells associated with only one of the two disks' colour.*

Demonstrators training - Demonstrators underwent 3 hours of fasting before every training session. In each trial the demonstrator was moved into the testing room and exposed to the novel foraging task for 30 minutes. A 10 minutes break was established between the first and second trial of the day. The training program was developed considering three consecutive phases (Fig. 2): the coloured disks were (*A*) positioned on the side of the wells containing food that was visible to the bird when approaching the well; (*B*) partially covering the wells so that the food inside was only visible at a close inspection; (*C*) fully covering the wells, preventing visual access to the food, so that birds could only access it by displacing the disks. During phases *A* and *B*, the learning criterion for demonstrators under training was that they visited at least three wells containing food in three out of four consecutive trials. Only then they proceeded to the next phase. In the final phase (*C*), the learning criterion was to visit at least three wells of the right colour that contained food, but not a single well of the wrong colour, in three out of four consecutive trials. If one individual did not reach the learning criterion after 25 trials of the same training phase, it was discarded as a possible demonstrator, and a new subject was chosen to start the training.

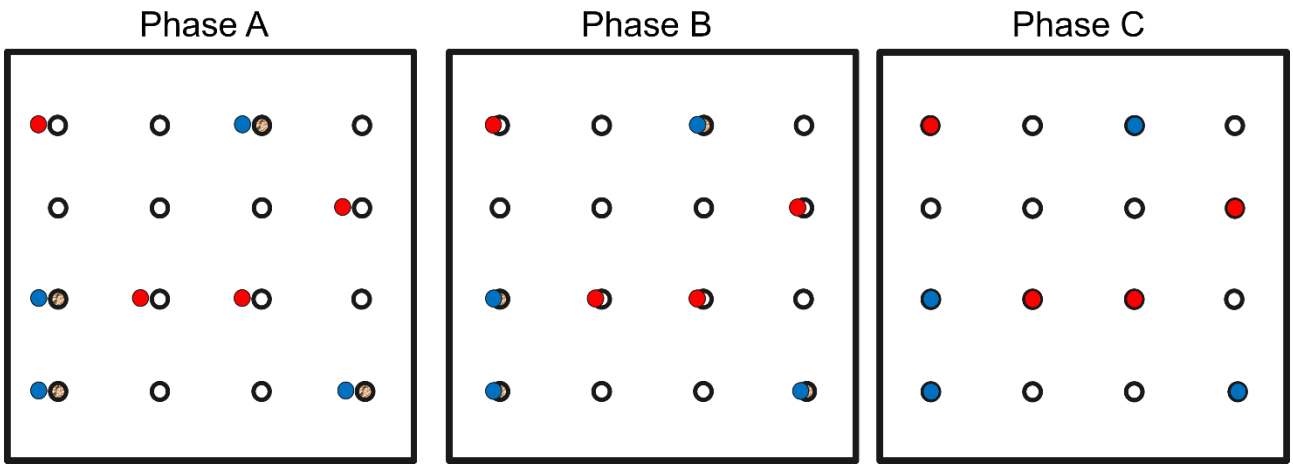

Figure 2: *Diagram of the three successive training phases; Phase A) Disks on the wells' side; Phase B) Disks half cover the wells; Phase C) Disks completely cover the wells.*

Social learning test

In this test, the observers were first individually allowed to observe a demonstrator interacting with the apparatus (*observation phase*), and where subsequently released to search for food (*performing phase*). Both the observer and the demonstrator were food deprived for 3 hours prior to the test, a reasonable time for birds of this size, in order to make them interested in searching for food. For the *observation phase,* the observer and the demonstrators were brought into the test room. During this *phase* the demonstrator had access to the foraging board while the observer was held in a small cage from where it could observe the demonstrator activity. The observer was kept in the cage to prevent it from distracting the demonstrator from the task. This phase lasted 30 minutes, after which both birds were removed from the testing room, and the board replaced by one with a new disposition of disks. The *observation phase* was only considered a successful learning opportunity - a necessary condition to proceed for the next phase - if the demonstrator visited at least three holes of the right colour and none of the wrong one. After a 10 minutes break, the *performing phase* was initiated, with the observer being released in the room and free to move around and interact with the foraging board for 1 hour with no interference. Observers were tested in consecutive trials until reaching the social learning criterion, that is to have found the food under at least the first three holes visited in at least three trials out of four consecutive ones. Observer were tested for a maximum of ten trials to learn and perform the new behaviour. The only exception was if a bird was one trial away from reaching learning criteria, in which case one extra test was performed.

A *control group* of 8 observers was tested in the same way, except that they were exposed to naïve demonstrators, that is, birds which were not trained as demonstrators, in order to determine how likely is that naive birds could learn to meet the learning criterion just by themselves. Achieving it, would provide a non-social alternative explanation for learning.

Memory retention

A subgroup of observers (n=9) that learned to perform the social learning test was re-tested 15 days after finishing the social learning task to assess their memory retention ability. These birds were placed in the testing room with the foraging board with a random distribution of disks as in a normal trial, for 30 minutes, after a 3 hours of food deprivation. Here each bird had the opportunity to eat from the covered holes, and the learning criterion was the same used in the social learning test.

Reversal learning

After the memory retention test, the same subgroup of observers took part in the reversal learning test. Here birds were exposed to the foraging apparatus as in the *performing phase* for other 10 trials of 30 minutes each. Only one major difference got introduced in the protocol:

the colour-food association previously learned by each subject was reversed. The criterion to succeed in the trial was the same as in the social learning test. Birds were considered proficient in reversal learning if they succeeded in two trials in a row.

Personality tests

Since some birds did learn the colour-food association and others did not, we decided to test if this difference between birds could be explained by differences in personality. Thus, a sub-group of birds (n=18) were subjected to personality tests in order to determine the presence of some personality traits related with reaction to novelty and sociability. Two standard personality protocols usually used with birds were applied to serins.

Novel object test

To measure boldness/shyness of birds, we performed a novel object test following a protocol similar to that of Kimball *et al.* (2022). It consists in exposing the subject to the presence of an unfamiliar object placed near the only feeder left in the cage for 15 minutes, after a period of food deprivation of 2 hours by removal of all feeders to standardize motivation. The protocol contemplates five trials per bird, three exposing the subject to different novel objects and two controls without any object. The objects presented were chosen to differ in shapes and colours to avoid habituation (see Supplementary materials), while the order of presentation was randomized. All trials were video recorder to avoid the presence of an experimenter in the room. Trials were carried out between 1100 hours and 1300 hours on different days, along a couple of weeks to assess the stability of the behaviour. The tests were performed in the home cage of each individual, so that the only novelty presented was the object (Fig. 3A). The video recordings were analysed using The Observer XT 10 program. Four variables were considered: the latency to perch near the object, the latency to perch on the feeder and the number of feeding events, to estimate neophobia, and the number of flight and hops as a measure of general activity.

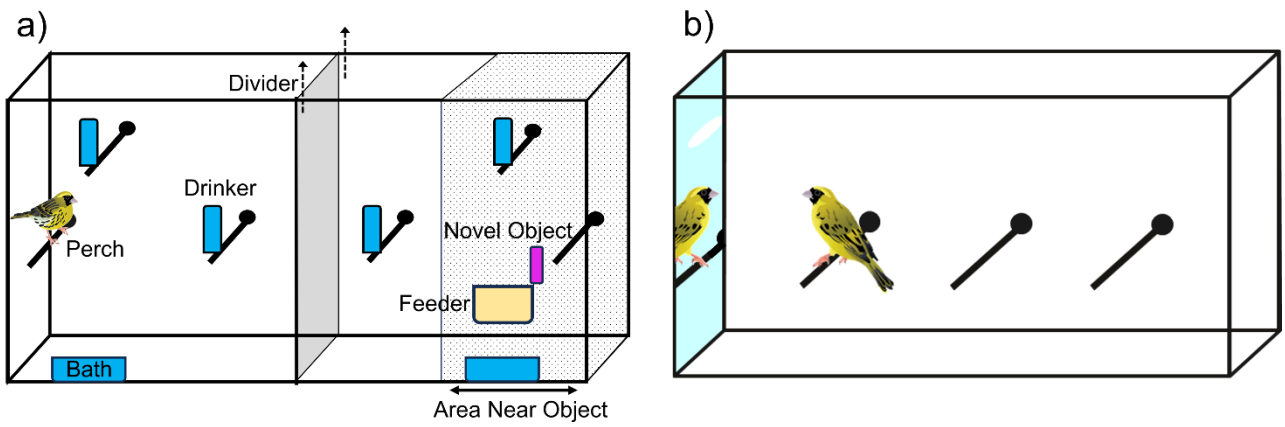

Figure 3: a) *Graphic representation of the Novel Object Test setup; the Divider was removed at the beginning of the test after a 2h starvation period.* ***b)*** *Graphic representation of the Mirror Test setup; the focal bird was placed alone in a cage with a mirror on one side.*

Mirror test

To measure individuals' sociability, we conducted a mirror test that simulates the presence of an unfamiliar conspecific through the use of a mirror. The test consists in keeping the focal individual alone in a cage with a mirror covering one of the sides of the cage that was initially hidden. The cage had 3 equally distant perches (Fig. 3B). A two-minute habituation time was established at the start, when the bird was positioned in the cage. The test lasted for 10 minutes, divided in two 5 minutes. parts. The mirror was covered by a cardboard during the first half of the test and was exposed by pulling a string to remove the cardboard. Trials were video recorded and analysed as in the novel object test. Six measures were collected in each part of the test: number of fast moves, time spent resting, time spent moving, time spent facing the mirror, mean distance from the mirror and number of pecks on the mirror.

Statistical analysis

Learning success was tested with a Fischer-Irwin Exact Test to determine if learning could be individual and not social, by comparing the outcomes of experimental and control groups.

A Generalised Linear Model (GLM) was used to test for the effect of the predictors on social learning results in which the dependent variable was the outcome of learning with a binary logistic distribution and identity as the link function. The social learning predictors considered in the model were: observer age and sex, demonstrator age and sex, morphology, and a two-way interaction between observer and demonstrator sex, the age and sex of the observer, and age of the observer and sex of the demonstrator. Memory ability was tested with a binomial test. Reversal learning ability was tested in relation to sex and age with a GLM.

Continuous personality variables were tested for normality, and a few were transformed to reach normality. The few variables that could not be transformed or were not binomially distributed were excluded from the analyses. The two latencies measured in the novel object test were very much close to binomial, and were transformed into such, thus describing if the subject did or did not get close to the feeder or the object. Time facing the mirror was square root transformed. General activity and 1/'time resting' were log transformed. The variables used as predictors in GLM were also tested for correlation.

Repeatabilities of the personality variables were tested using the rptR package (Stoffel et al. 2017) for R v4.3.1(R Core Team, 2023). A few custom scripts were adapted from the example proposed by Stoffel *et al.* (2019).

The control trials of the personality tests were used to determine if the variables did measure behavioural response to stimuli. For that purpose, a Generalized Linear Mixed Model (GLMM) was performed, with Bird ID as a random factor, and the test nature (control vs experimental) as a fixed factor; a significant effect of the fixed factor would indicate the variable was capturing what was being measured in the personality test.

The personality variables that showed repeatability were aggregated in two PCA, one for each of the personality tests, to obtain an index for subsequent analysis. We used the eigenvalues superior to 1 criterion to retain factors. One principal component was retained from each PCA, which became the Sociability Index and the Boldness Index. These indexes described each bird location on the personality spectrum and were used to test whether personality could explain

the outcome of social learning, through a GLM with learning as a binary logistic dependent variable, as above, and the personality traits as predictors.

Ethical note

All experimental procedures conducted on the birds comply with Portuguese and European laws regarding scientific testing on animals. The capture of birds and their subsequent maintenance for the experiments of this project were carried out under permits N°09/2021/CAPT and Nº 049/2023/CAPT to (Author name), by ICNF, Instituto da Conservação da Natureza e das Florestas, I.P. Research was also assessed and approved by the body responsible for the well-being of animals in CIBIO-BIOPOLIS (2024/03). No bird was subjected to any act of mistreatment or neglect. Sampling was conducted making use of fine-mashed mist nets that were inspected every 20 minutes to minimize the harmfulness of the process. All birds were accompanied and monitored daily by the authors of this work throughout their seven-month captivity period. To minimize distress a limit of 4 hours of food deprivation per day was set, also individuals that partake in aggressive interactions were moved to different cages to prevent future ones. At the end of the experimental procedures, all birds were released in the same locations where they were captured.

RESULTS

The tests conducted confirmed the presence of social learning in serins, however only some birds were successful observers. Sex, age and personality traits were unable to explain the observed differences in social learning. All learners were then capable of remembering the knowledge acquired for at least 15 days, while cognitive plasticity in reversal learning was limited to part of the subjects.

Social learning

Of the 35 birds that were tested after observing experienced demonstrators visiting the holes covered with the appropriate colour disks, 14 of them (40%) learnt to perform the feeding task, learning to associate the disk colour with the presence of food (Fig. 4). To rule out the possibility that these birds learned autonomously and not by observation of others' behaviour, we submitted a number of birds to naïve performers that had not learnt the colour-food association and could not provide them with clues for finding food. All the 8 observers of the control group were unable to learn by themselves how to solve the novel foraging task (Fig. 4). The difference between the two groups was significant (Fisher-Irwin exact test: p=0,039), confirming that observers learnt the task by observation.

The majority of observers (11 out of 14) took from 8 to 11 trials to learn (Average = 9). However, three of them (21%) were very quick to learn, having done it between the 3rd and 5th trial. So, there was some heterogeneity on how fast they were capable of learning.

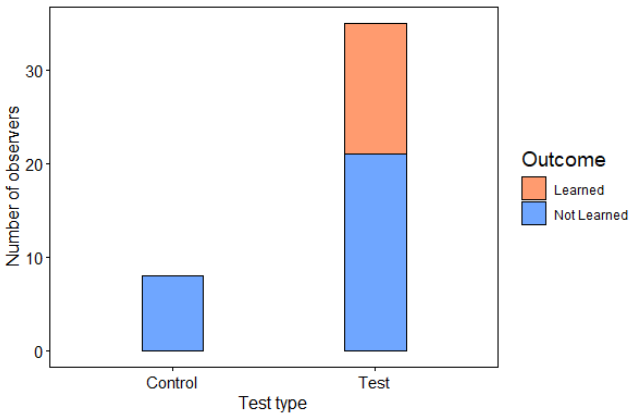

Figure 4: *Outcome of the social learning test for the Control group (N=8) and the Test group (N=35).*

We considered sex and age of both demonstrators and observers as possible explanatory factors for differences in learning ability. Learning was not significantly affected by either sex or age of demonstrators and observers or the interaction between them (Table 1). However, we found a non-significant tendency for the interaction Age O * Sex D on social learning (Table 1). Particularly, we observed that older observers had only around 10% rate of learning from a male demonstrator, contrasting to young observers that learned in more than 60% of the cases from males (Fig. 5). Bird morphology, represented by two PCs. PC1, which accounts for wing length variation (Annex 1), was a significant predictor of social learning (B=1.396, p=0,038). That is, birds with longer wings were more capable of learning by observation. This difference in wing size is irrespective of birds age and sex, since these factors were included in the model.

Table 1: Results of the Generalized Linear Model on the outcome of social learning test, comparing social learner and non-learners. Bold type indicates a significant result. DF is equal to one for every predictor tested. B is the slope for the continuous predictors.

Predictors	Estimated means	Standard errors	Likelihood Ratio $\chi 2$	*p*	B
Age O	1Y 0.57 AD 0.74	0.186 0.128	0.556	0.456	-
Sex O	F 0.72 M 0.59	0.164 0.206	0.202	0.653	-
Sex D	F 0.57 M 0.74	0.165 0.142	0.603	0.437	-
Age D	1Y 0.64 AD 0.68	0.181 0.176	0.026	0.873	-
PC1 Morph	-	-	**4.297**	**0.038**	**1.396**
PC2 Morph	-	-	0.632	0.427	-0.394
Age O*Sex O	-	-	0.309	0.578	-
Age O*Sex D	-	-	2.942	0.086	-
Sex O*Sex D	-	-	0.014	0.907	-

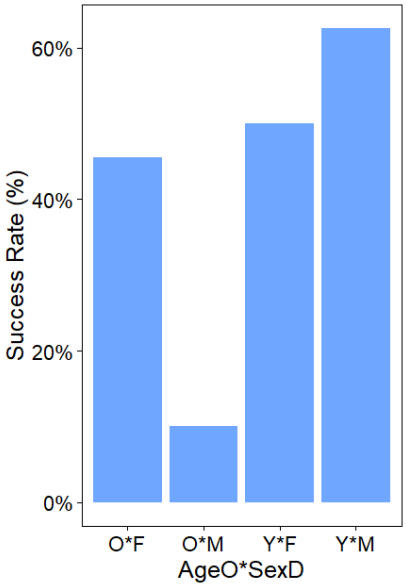

Figure 5: Learning success rate comparison between each category of demonstrator sex and observer age. Y= Young <1 years old; O= Old > 1 years old; F= Female; M= Male.

Memory and reversal learning

A group of nine observers (Subgroup1) was tested for memory retention 15 days after the ending of the social learning test. All of them succeeded in the foraging task (binomial test p=0.004), indicating that all birds retained in their memory the association they have learnt before.

Subsequently, the efficient learners were exposed to a reversal of the association rule, by placing the food under the other colour, in a reversal learning colour-food association. Of the nine birds tested, 4 (44%) were capable of reversing the previously learnt rule. Age or sex did not explain the differences in reversal learning ability of the observers (Table 2).

Table 2*:* Result of the Generalized linear model on the outcome of the reversal learning test, comparing individuals for sex and age.

Variables	Wald	p
Sex	0.083	0.773
Age	0.083	0.733

Personality

A sub-group of the birds tested for social learning was also tested for personality in order to assess if the differences between social learners and non-learners could be explained by

differences in their personality. For this purpose, we considered two standard personality tests that relate with novelty and sociability: the novel object test and the mirror test.

Table 3: *Results of the repeatability test for each personality variable from the two personality tests. Type of distribution of the variables is indicated. R= Repeatability index; higher values indicate higher interindividual Repeatability. Bold type indicates high repeatability scores (R>0.5). In brackets are indicated the type of transformations applied to the respective variables.*

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Variables	Test	Distribution	R	p
Time Facing Mirror (sqrt)	Mirror	Normal	**0.589**	0.0017
Time Resting (Log_inv)	Mirror	Normal	**0.658**	0.0004
General Activity (Log)	Novel object	Normal	**0.504**	0.0003
Perch Near Object	Novel object	Binomial	**0.711**	0.0010
Perch on Feeder	Novel object	Binomial	0.302	0.0486

Novel object test

Intra-individual repeatabilities were measured for each of the variables selected as proxy for neophobia/neophilia. *General Activity* and *Perch Near Object* were highly repeatable (R>0.5) (Table 3). The time *Perching on Feeder* was less repeatable and only marginally significant (R=0.302, P=0.049). We tested the variables for correlation (Annex 3), and we found that the variable *Perch Near Object* had a positive but marginally non-significant correlation with *Perch on Feeder* (0.477, P= 0.053), it also had a negative marginally non-significant correlation with the *General Activity* (-0.471, P= 0.056). This indicates out that more active birds tend to be less prone to get close to the novel object. We found no significant correlation between *Perch on Feeder* and the *General Activity* (-0.205, P= 0.429). However, *General activity* was not significantly affected by the presence or absence of the novel object, so that it is not associated with boldness, contrary to the other two variables (Annex 4).

Mirror test

In the mirror test there was high repeatability (R>0.5) for *Time Facing Mirror* and *Inverse of Time Resting* (Table 3), indicating individuals behaved consistently across the two test trials. The two variables were negatively correlated (-0.590, P=0.013), so that birds that spent more time facing the mirror were also those who spent more time resting (Annex 3). Both variables were significantly affected by the test nature (control or not), thus revealing to be capturing the sociability trait (Annex 4).

A correlation analysis between the variables of the Mirror Test and the Novel object test was not significant for all variables (Annex 3). Thus, boldness and sociability are probably not part of a personality syndrome.

Personality and social learning

We performed two Principal Components Analyses (PCA) to produce indexes for novelty avoidance and for sociability. The Principal Component (PC) extracted from the Mirror test variables had positive loadings (0.892) on the *Inverse Time Resting* and negative (-0.892) on the *Time Facing Mirror*. Thus, in our Sociability Index a lower score meant a more sociable individual. The PC obtained for the Novel Object test had a positive loading (0.946) on both latencies, *Perch Near Object* and *Perch on Feeder*. Thus, in our Boldness Index, a lower score meant a more curious individual. Both learners and non-learners have, on average, similar personality indexes. However, individuals that did not learn have a wider distribution of values for boldness than learners (Fig. 6a). Learners, have a wide distribution of sociability values (Fig. 6b). Neither the sociability nor the novelty indexes had any explanatory value for the differences in learning ability of the birds (Table 4).

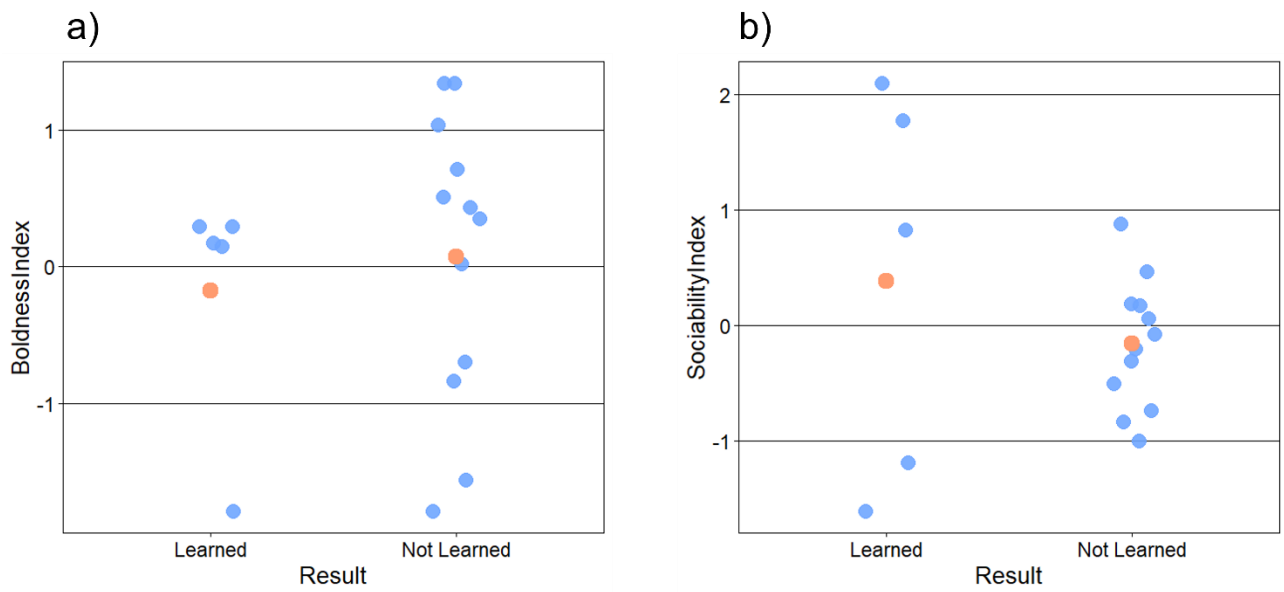

Figure 6: Scatter plots of the personality traits of successful and unsuccessful social learners. a) Boldness Index; b) Sociability Index. Orange dots represent mean values.

Table 4: Results of the Generalized Linear Model on the binomial distribution between social learners and non-learners. The predictors tested are the two personality indexes.

Predictors	Likelihood Ratio $\chi 2$	p.	B
Boldness Index	0.824	0.364	-0.005
Sociability Index	0.000	0.994	-0.579

DISCUSSION

We found evidence of social learning in serins, a gregarious, granivorous small passerine bird. Individuals revealed considerable variation in this cognitive skill, so that less than half managed to succeed. Learning was not predicted by sex or age of learners or demonstrators. However, birds with longer wings were more proficient in social learning. Maybe, longer wings have an impact on the bird's efficiency to collect energy and resources necessary for growing. We also show that serins' memory was still in place after fifteen days, with birds being capable to remember the associative rules learnt. Part of the learners were also capable of reversal learning, a much more difficult cognitive capability. Serins behave consistently throughout context and time with each individual exhibiting personality traits distinguishable from its conspecifics. However, these behavioral interindividual differences are not associated with the individual ability and reliance on social learning.

Demonstrators training

We succeeded in training serins a colour-food association through a protocol with a gradual increase in the association difficulty (Aplin et al., 2013; Chantal et al., 2016) many of whom made use of foraging boards or similar apparatus to test the ability to understand a colour-food association (Ashton et al., 2018; Caves et al., 2018; Heyes and Saggerson, 2002). During the training the demonstrators took on average more attempts to learn in phase (A) than in the other phases, even though in principle this was the easiest, because the food was visible. This learning pattern, and the fact that some individuals never interacted with the testing apparatus, suggests that the harder step was to get accustomed to the presence of a novelty, a novel object in a new environment.

Social learning

In the last few decades many studies on social learning have broadened our understanding of this behaviour in an increasing number of animal species with different ecologies and life history traits (Hoppitt & Laland, 2013). Here we demonstrated that a granivorous and gregarious bird species, such as the Serin, significantly relies on social learning in a foraging context. Indeed, a relevant proportion (40%) of the individuals involved in the study was capable to learn a complex foraging technique involving learning a colour-food association in less than 300 minutes of exposition to a capable demonstrator. Although very different in their foraging habit, blue tits, were observed to perform in a social learning study that also involved a colour-food association similarly to serins (54% learned) (Aplin et al, 2013). Our finding thus expands our knowledge on social learning skills from insectivorous hunters also to granivores.

Birds in the control group, where they were allowed to observe a naïve bird, not a demonstrator, were unable to learn the association task. Because control observers were not able to learn even if exposed to naïve demonstrators, we could also exclude that learning occurred as a form of social facilitation, confirming that the observers learned by social learning. However, our testing apparatus allowed birds to accidentally remove the disks covering the wells just by walking or landing on the foraging board. We argue that this event may have played a role during the trials of three of the individuals (two test and one control subject). These birds were very interactive with the testing apparatus and, during one of their first trials, they accidentally found out of the food presence. Since then, they increased the number of disks indiscriminately displaced within each trial. However, they did not prove to have learned the association between the food presence and the colour of the disk. Even so, this inefficient strategy made them capable of always finding food by removing almost all disks. These three

cases made us think that more than one foraging strategy could be learned by the observers, i.e. food is present under some disks. An element that could have favoured the establishing of this simpler rule was that displacing indiscriminately right and wrong disks was not costly enough in terms of time and energy invested. This observation highlights the fact that serins, even if they are clever individual learners, can learn more complex and efficient behaviours through social learning, recently a similar result was observed in bumblebees where individuals were able to socially learn a task too difficult to learn individually (Bridges et al., 2024). These finding point towards the idea that sociality drives intelligence, and at least that social learning favours individuals in a foraging context because it allows them to gain information on food availability in different land patches from the conspecifics they gather with.

However not all individuals made use of social learning, so we set out to investigate which individual characters may explain this event. In a few other animal species, the sex of the observers is a reliable predictor of social learning. Female blue tits exposed to a demonstrator had higher learning success rate than males, with percentage of individual that learned around 61% for females and 30% for males (Aplin et al., 2013). Similarly, females are faster social learners in two species of lemur (Kappeler 1987; Schnoell and Fichtel, 2012). In serins, out of the 14 individual that learned, nine were females (64%). What we obtained is in line with the results observed in blue tits, in terms of proportion, but nonetheless we did not find any statistically significant support to the idea that the sex of the observer is a predictor of learning. Still, the probability was too high to think that an effect could be discernible by enlarging the sample size. Age is another factor commonly associated with social learning. Juveniles and young adults were the most successful social learners within lizards (Noble et al., 2014) and meerkats (Thornton & Malapert 2009). While in birds contrasting results emerged from successive studies on blue tits, with the most recent proving no effect of age on learning (Alpin 2013; 2015; Penndorf & Aplin, 2019). In Serins, our results showed that young adults constituted 57% of the successful individuals, which is not significantly different from older birds. We had, however, a non-significant tendency indicating that older birds tended to learn less from males. Another study suggest that young males are better innovators but worse at spreading knowledge (Cadieu, 2010). Maybe they are not considered as reliable sources of information.

We found that birds with longer wings learnt more often. As far as we know it is the first time in the literature that a morphometric character is predictor of social learning. Why would this morphometric parameter predict social learning abilities? A possible explanation is that being a better social learner makes individuals more efficient in foraging, thus allowing to invest more energy in developing longer wings. In fact, in this species, wings continue to grow during all adult life and not just during the early development (Mota, personal observation). This characteristic could support the idea that serins invest in wing length if they have enough resources to do so. However, this hypothesis opens many questions. Why specifically the wings? While not perhaps other body parts? Why should a small difference in wing length be adaptive and worth to invest in? Could dominance have a role in this relationship? For instances, individuals with longer wings may be dominant and at the same time may be the better social learners because they gain profitable experience observing subordinates, that according to the “Necessity drives innovation” hypothesis are usually forced to be better innovators (Arbilly and Laland, 2017; Thornton & Samson, 2012). Male serins display feather patches which/whose carotenoid colouration is related with dominance (Leitão et al., 2015), yet the influence of dominance on social learning has not been studied in this species.

However, male blue tits were found to be affected by hierarchical relationship between observers and demonstrators (Aplin et al., 2013). In fact, dominant aggressive interactions between males are common in avian species. Moreover, male canaries when tested for social learning were negatively affected by aggressive interactions with male demonstrators (Cadieu, 2010).

Cognitive skills

The cognitive skills of a subgroup of the successful observers were tested further. First, we wanted to know if there was memory retention of what was learnt. After 15 days, the memory retention was solid, as all individuals succeeded in the foraging task. Proficient memory is a trait observed across many passerines from Corvidae (Tomback, 1980), and Paridae (Sherry, 1984), to Estrildidae (Ueno & Suzuki, 2014). However, our finding further extends this evidence to true finches (Fringillidae). This ability is useful to remember the distribution across the foraging area especially during the winter season.

Furthermore, when these individuals were exposed to a reversal learning test 44% of them were able to reverse the associative rule previously learned. Comparable results were obtained also in great tits, where 59 % of captive individuals succeeded in the reversal task, although not resulting from social learning (Cauchoix et al., 2017). Other studies on avian species found individuals to differ in reversal learning success or in reversal learning speed (Laschober et al., 2021; Zidar et al., 2018; Benedict et al., 2022). However, differences in the experimental designs makes comparisons scarcely meaningful, due to differences in the number of trials given to reach the learning criterion, and in the task to complete. The reversal learning ability revealed by serins has potential fitness consequences since cognitive plasticity is very important to cope with an everchanging environment. It is, thus, a skill that can be positively selected in these birds' populations. While in some species females were found to perform better in reversal learning test (Petrazzini et al., 2017), we have no indication for a sex difference in serins, although the sample size is too small to draw conclusions.

Personality

The strong repeatability found on the personality traits we tested further support the existence of stable behavioural differences related to personality in Serins, as a previously found (Leitão, 2011). Our results indicate that boldness and sociability do not affect significantly social learning in serins. We predicted that bolder individuals would have an advantage in this learning setup because it involved the interaction with a novel object and environment, hence less neophobic individuals would have been less stressed during the tests. Besides, we expected more sociable individuals to be better social learners because they would interact and observe more the demonstrator they were paired with. Previous literature on the interactions between personality traits and social learning was unable to depict a clear pattern, across the different species and testing conditions studied. The enormous difference between the learning test protocols and the great diversity in ecology and life history traits of the studied species (from insects to birds, to primates) makes it extremely challenging to compare the results between studies on this topic. Even considering only the avian species studied, researchers found contrasting results: more explorative great tits performed better at social learning (Marchetti and Drent, 2000) while bolder and more explorative geese rely less on social information (Kurvers et al, 2010).

We selected a small number of personality tests, but that were adequate for the context of social learning. Maybe, other personality traits could be related with differences in learning ability, or maybe that ability has no relation to personality in any way.

Conclusion

In conclusion our study showed that serins are capable of social learning in a foraging context. This study widens our knowledge on how widespread social learning is in non-social animals, by investigating a gregarious, granivorous avian species. Serins not only learnt associative rules but also remembered them over short period of times, and some individuals were capable of reversal learning. Social learning abilities in Serins, as in other bird species, are extremely variable between individuals, even among those that belong to a single population. We investigated this interindividual difference and found no evidence of it being related to sex, age or personality. We found a positive relationship between social learning success and wing length; therefore, we hypothesize that social learning adaptiveness might increase foraging efficiency and thus translate in a higher amount of energy that the individual can invest in growing. To clarify this interaction further studies on the actual impact of social learning on individual fitness would be required, including dominance.

Data Availability

Data will be available at Zenodo:

https://zenodo.org/badge/DOI/10.5281/zenodo.14476756.svg)](https://doi.org/10.5281/zenodo.14476756

Declaration of Interest

None

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AUTHOR CONTRIBUTION

A. F.: Conceptualization, Methodology, Formal analysis, Resources, Data curation, Writing - original draft, Visualization. **R. S.**: Conceptualization, Methodology, Investigation, Formal analysis, Resources, Data curation. **P. G. M.**: Conceptualization, Methodology, Investigation,

Validation, Resources, Writing – review and editing, Visualization, Supervision, Administration, Funding acquisition.

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Appendix

Table A1: The component matrix of the Principal Component Analysis conducted on the morphometric variables. Two components are extracted, in bald type are the main loading for each component.

Component Mtrix		
Moprhometric mesures	**Component**	
	1	**2**
Left wing	**0.964**	0.094
Wright wing	**0.961**	0.132
Tarsus	0.007	0
Beak hight	0.069	**0.629**
Beak Lenght	0.428	**-0.613**
Beak widht	0.001	**0.876**

Table A2: Component loading of the personality variables used to compute the personality indexes. Positive loadings indicate that the variable is positively correlated to the index, negative loadings indicate the opposite.

Test	Variable	Component loading
Novel object	Perch on Feeder	0.946
Novel object	Perch Near Object	0.946
Mirror test	Time Faceing Mirror	-0.892
Mirror test	Time Resting	0.892

Table A3: Pearson Correlation between the selected personality variables. In the first row is the Pearson correlation value, in the second row the significance (two-tailed). Asterisks indicates significant correlations with a 95% CI, double asterisks indicate significant correlations with a 90% CI.

Personality variables	Time Facing Mirror	InvTime Resting	General Activity	Perch Near Object	Perch on Feeder
Time Facing Mirror	1	-0.59 0.013*	0.063 0.809	-0.157 0.546	-0.058 0.825
InvTime Resting	-	1	-0.139 0.594	0.306 0.232	-0.151 0.562
General Activity	-	-	1	-0.471 0.056**	-0.205 0.429
Perch Near Object	-	-	-	1	0.477 0.053**
Perch on Feeder	-	-	-	-	1