INDIVIDUAL VARIATION AND LEARNING IN CRICKETS

By

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Abstract: Learning can play a key role in an individual's fitness. Learning also often varies among different individuals of the same species, with some individuals being faster learners in different situations such as being better at reversal learning or initial associative learning. There are a variety of factors that might explain such variation, including animal personality. This study aimed to look at how personality traits commonly found on the reactive and proactive axis, such as aggression, neophobia, and latency to exit, affect an individual's learning strategy. In particular, I looked at whether more proactive individuals were faster at learning initial learning, and slower at learning reversals compared to more reactive individuals. I also looked to see if more proactive individuals were less likely to socially learn compared to more reactive individuals.

To test whether different personalities have different learning strategies I used the house cricket, or *Acheta domesticus.* The crickets, both male and females, ran aggression, novel object, and latency to exit trials. For the learning trials the crickets had to learn to associate two different odors with either a reward or a punishment, and upon learning an association the odors would be switched, so that the reward that was with one odor was then paired with the other odor. There would be two such reversals. Only female crickets were used for the social learning trials, where they were placed in a maze with a stimulus cricket and had to learn to associate an odor that was brushed on the stimulus with a reward.

In the end, no social learning was found in the female crickets. With regards to the personality and learning strategies, it was found that individuals that took longer to exit their shelter were faster reversal learners and faster at initial learning as well. Males were also significantly slower learners in the second reversal compared to the females, while at the same time males were faster learners in the initial learning experiment and the first reversal. The initial learning speed was significantly correlated with the first reversal as well.

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CHAPTER I

PERSONALITY AND INDIVIDUAL VARIATION IN LEARNING IN *ACHETA DOMESTICUS*

INTROUCTION

Individual Variation and Learning

Learning, from simple associations to complex social interactions, has played an important role in animals' abilities to adapt to their environment (Shettleworth 2010). Recently, it has even been proposed that learning is a trait shared by all animals with a nervous system (Hollis & Guillette 2015). Learning is defined as a change in behavior, caused by experience, that is detectable at a later time (Rescorla 1988). Learning could convey fitness benefits, such as allowing individuals to develop better foraging strategies to respond to changing conditions of food availability (Pontes et al. 2019). For example, in grasshoppers, *Schistocerca americana*, some individuals were faster at learning to associate a particular color with more nutritious food, allowing them faster growth (Dukas & Bernays 2000). In starling chicks, *Sturnus vulgaris*, individuals that were able to solve a learning task faster were more competitive and had a higher social rank (Boogert et al. 2006). However, learning is also costly, leading to trade-offs between learning and other traits, which may affect the net fitness benefits of learning. For example, faster learners had worse competitive abilities as larvae in Drosophila melanogaster (Mery & Kawecki 2003), and better learners were less fecund in cabbage white butterflies, Pieris rapae (Snell-Rood et al. 2011). In order for learning to have evolutionary consequences in response to selection, there must be some level of individual variation in learning, and many studies have shown such variation

(Guenther et al. 2014, Naworth et al. 2017, Sommer-Trembo & Plath 2018). Understanding the factors that affect individual variation in learning can help us understand how natural selection might act on learning ability (Boogert et al. 2018).

There is currently much debate about the factors that generate inter-individual differences in learning ability (Boogert et al. 2018). Individual variation in learning could arise because of genetic differences between individuals. This can be assessed by measuring the heritability of learning ability, or the proportion of phenotypic variation in learning that is due to genetic variance (Boake 1989). In one example, chimpanzees, *Pan troglodytes,* also have shown heritability in learning, with spatial learning in particular being highly heritable (Hopkins et al. 2014).

There have also been several studies that look at developmental plasticity in learning (Morand-Ferron et al. 2016, Lambert & Guillette). Animals that grow up in a more isolated environment, especially if they are social animals, may have reduced learning performance (Ashton et al. 2018). The physical environment can also play an important role: for instance, juvenile *Pungitius pungitius*, the nine-spined stickleback, use chemical and visual information when deciding which shoals to join. Juveniles that were raised in a visually restricted environment relied more on chemicals when presented with both chemical and visual cues compared to juveniles that were raised in a relatively clear water environment (Pike et al. 2018).

Another effect on individual variation on learning could be an individual's personal experience. Individuals that have more experience in a task can perform the task faster than its conspecifics

(Dhawan et al. 2019, Komischke et al. 2002). A study of North island robins, *Petroica longipes*, found that robins that engaged in a problem solving experiment that involved flipping a lid upwards were faster learners at a similar experiment that involved a swivel lid (Shaw 2017).

Animal Personality and Learning

Animal personality, defined as consistent inter-individual differences in behavior across time (Réale et al. 2007), is likely an important source of individual variation in learning (Boogert et al. 2018). If individual differences in behavior are consistent across time, then the behaviors exhibit repeatability. Repeatability is defined as the proportion of variance in a behavior that is attributable to differences among individuals (Lessells & Boag 1987) and is often used to determine whether a trait can be considered a personality trait (Dingemanse & Wright 2020). As a result of personality differences, individuals of the same species will consistently vary in their behavior, even when placed in the same situation (Sih et al. 2015).

Personality can also act as a constraint, preventing individuals from displaying optimal behaviors in all situations (Sih et al. 2019). For instance, carry-over effects take place when behaviors are beneficial in one context but sub-optimal in others, such as aggressive behavior towards potential mates (Maupin 2001), or a lack of caution when predators are present (Pintor et al. 2008). An example of a carry-over effect of aggression can be seen in desert spiders, *Agelenopsis aperta*, in which females that attack prey more readily are also more likely to eat potential mates, thus negatively affecting female reproductive success (e.g., Maupin 2001).

One of the personality traits that might affect learning is aggression. There is often consistent, repeatable individual variation in aggression (Santostefano et al. 2016). For this study, aggression will be defined as “actions that are presumed to be motivated by resource control, directly or indirectly” (Blanchard et al. 2009). Since agonistic behaviors are important for obtaining resources by winning contests (Hofmann & Schildberger 2001), less aggressive individuals may use alternative strategies to obtain resources.

In particular, the ‘necessity drives innovation’ hypothesis proposes that there is a trade-off between aggression and both learning and the expression of innovative behaviors: individuals invest more in learning or innovate new behaviors because they were unable to obtain resources via competition (Laland & Reader 1999). This trade-off has been shown in great tits, *Parus major,* where less competitive birds spent less time at bird feeders but were better at obtaining food by novel problem solving (Cole & Quinn 2012). Aggression may also interact with learning through carry-over effects. For instance, aggression might covary with learning strategies, with more aggressive individuals favoring a fast-learning strategy as opposed to a more flexible one (Sih & Del Giduce 2012). This has been shown in cavies, where more aggressive and exploratory individuals were faster at learning initial associations but were slower at reversal learning (Guenther et al. 2014).

An individual’s willingness to explore and take risks is considered to be part of the proactive-reactive axis and is often found to be a repeatable personality trait (Sih et al. 2004). One way to measure this is through latency to emerge trials, where an individual is put in a shelter or a “safe place” and the time it takes for that individual to leave its shelter is measured (Niemela et al. 2012 A, Niemela et al. 2012 B). More proactive individuals tend to leave their shelter faster than more reactive individuals (Sih et al. 2019), and this behavior may relate to learning style if it makes them faster, but less flexible, learners (Sih & Del Giduce 2012).

This has been shown in rodents, *Myodes glareolus,* and *Cavia aperea* , where the more proactive individuals were faster at initial learning but had slower reversals compared to less proactive individuals (Guenther et al. 2014, Mazza et al. 2018). That said, not all studies found that differences in boldness were related to variation in learning (Sommer-Trembo & Plath 2018).

Another personality trait that may affect learning is neophobia. Neophobia is often quantified as the time it takes for an organism to approach a novel object (Bebus et al. 2016), and this behavior is often repeatable (Verbeek et al. 1994, Greggor 2020). Neophobia has been used as a covariate in numerous learning studies as a proxy for variation in the proactive-reactive axis (Mazza et al. 2018, Bebus et al. 2016). Animals with high levels of neophobia have been suggested to be more sensitive to environmental change and thus be more reactive and flexible, making them faster at reversal learning (Sih & Del Giduce 2012). However, similar to aggression, neophobia has been found to have mixed effects on learning, with some studies showing that neophobic individuals are better at reversal learning (Bebus et al. 2016), some showing neophobia is correlated with worse reversal learning performance (Guido et al. 2017), and other work showing no correlation whatsoever between neophobia and reversal learning (Gibelli & Dubois 2017).

Hypothesis

Crickets as a whole are an excellent group of species to study the relationship between personality and learning. The ethogram for aggression is well documented in many cricket species (Adamo & Hoy 1995, Bertram et al. 2011), and aggression has been shown to be repeatable (Santosefano et al. 2016). Latency to emerge has also been shown to be rank-order repeatable in *Gryllus integer* (Niemelä et al. 2012). Crickets have also been used in learning studies, and *Gryllus bimacultus* are able to perform associative olfactory learning (Mastumoto & Mizunami 2000, Mastumoto & Mizunami 2002). In this experiment, I tested the relationships between different potential components of the proactive-reactive axis -- aggression, neophobia and the latency to emerge from a shelter -- on learning speeds in both associative and reversal learning in male and female house crickets, *Acheta domesticus.*

Based on the speed-flexibility trade-off hypothesis (Sih & Del Giduce 2012), I predict that individuals that are more aggressive, less neophobic, and faster to emerge from a shelter will have a faster learning speed during initial learning but will have a slower learning speed in the subsequent two reversal learning experiments.

METHODS

Subjects

The crickets used for this experiment were adult *Acheta domesticus.* They were either bought as one to three-week-old immature individuals from Fluker's Farm (Port Allen, LA) or were raised in the laboratory. The laboratory raised crickets were hatched from eggs laid in containers that were 20.32cm x 20.32cm x 7.63 cm and filled with potting mix. The soil was kept damp, but not muddy. After the crickets hatched, they were moved to a group container that was 65.4cm x 46.7 cm x33.7 cm and kept at 25 degrees Celsius. The group container had egg cartons for shelter, and water vials with cotton for water. The crickets were given chicken feed (Nature Wise Layer Feed, 16% Protein Pellet) for food. In addition to the chicken feed, the crickets were given lettuce for the first four weeks of their lives as an extra source of food and water. Food and water were replaced twice a week. Once the crickets reached maturation, they were placed in individual, transparent, plastic containers that were 20.32 cm x 20.32 cm x 7.63 cm, with the first eighty crickets to mature (40 females and 40 males) being used for the trials. The containers were often stacked on top of each other, with each container also containing holes for air. Each individual container contained an egg carton, a water vial, and a petri dish for food.

Aggression trials

Twenty-four male crickets and twenty-six female crickets were randomly selected to be focal individuals (i.e. those individuals from whom I estimated aggression scores and later measured learning) using a random number generator in R (R core team, 2019).

The remaining fifty were used as “stimulus crickets” (i.e. those individuals that were used as opponents for the focal crickets) for the aggression tests. The focal and stimulus crickets were grouped in blocks of five, with five focal and five stimulus crickets that had no more than a twenty percent difference in body mass. This was because body mass has been shown to play a significant role in the outcome of contests in crickets (Hack 1997). Each focal cricket competed in five trials on different days, facing off against a different stimulus cricket each time. By having each cricket run five trials I was able to get an estimate for the repeatability of aggression. By having a different opponent face off against the focal cricket each time, the effects of the specific opponent on the measured aggression in the focal cricket should be reduced. Due to each cricket only doing one trial per day, any “winner” and “loser” effects should have dissipated before the next trial (Rillich & Stevenson 2011, Iwasaki et al. 2006). used as “stimulus crickets” (i.e. those individuals that were used as opponents for the focal crickets) for the aggression tests.

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The aggression trials consisted of two crickets, one focal and one stimulus, being placed in a small arena for five minutes, where their interaction was recorded with a Sony DCR-SR85 handycam. The stimulus cricket was identified by a red paint mark on the pronotum.

The crickets were placed in two plastic cups where they were given two minutes to acclimate to the arena before the trial began. After each trial, the crickets were weighed, and the arena was wiped clean with ethanol. The scoring of behaviors was based on Adamo and Hoy (1995). Each behavior was given a specific weight corresponding to the level of aggression associated with that behavior, and each time the cricket performed that particular behavior it was recorded (Table 1). The duration of each behavior was also recorded so that a cricket's end aggression score for a trial was the score for a behavior multiplied by the amount of time that the cricket spent performing that behavior. For instance, if a cricket did two mandible flares for a total of five seconds it was given an aggression score of fifteen, as the mandible flare has a score of three and the time it spent performing the behavior was five seconds. Aggression songs were recorded but were not included in the final score because including these dramatically inflated the score of some individuals, and because sometimes individuals called in the absence of other aggressive behavior, making it unclear whether calls were being used in an aggressive context. All videos were watched and scored using Boris software, which allows for the user to keep track of the number and timing of behaviors (Friard & Gamaba 2016).

Neophobia and latency to emerge

Neophobia was quantified by measuring the response of each cricket to novel objects. Individuals were placed in a plastic container that was 61cm x 47cm x 40cm. In the container, there was a shelter and a novel object (a PVC pipe for the first test and a bottle for the second). The shelter was placed in the corner of the container, with the novel object being placed at the center of the opposite end (see figures 1.1 and 1.2). The crickets began the trial in a shelter which the cricket could leave at any time, and the time it took to leave the shelter (latency to emerge) was recorded along with the time it took until it touched the novel object (neophobia score). Each individual was given ten minutes to come into contact with the novel object with its antennae on each trial. Individuals were tested in a random order.

After each trial, the arena was wiped down with ethanol. Each individual was tested twice, once for each of the two novel objects. Two scores were taken: the exit score, which was the time it took for the cricket to leave the shelter in the arena, and the touch object score, which was the time it took for the cricket to come into contact with the novel object. The scores for the two trials were averaged, giving a cricket an average exit shelter time and an average touch object time.

The apparatus and the general setup

The learning trials used the same focal crickets as the aggression and neophobia trials. The learning design was a discrimination learning experiment in which the cricket must learn to associate an odor with a water reward. Individuals were water-deprived for 24 hours before testing to ensure motivation to participate. Learning trials took place in a t-shaped maze that had tubing going to two separate containers, with a tee being used as the starting point for the maze (see figure 2). The maze was made up of 5.08 cm diameter tubing that was roughly 45.72 cm long starting from the tee and ending in a clear container that was 33.35cm x 19.38cm x 11.43 cm. Each side contained an odor (a cotton ball soaked in either 1ml of vanilla or 1 ml of strawberry extract, both of which can be detected by crickets (Matsumoto & Mizunami 2006)). One odor was always associated with the reward (water), and the other was associated with a non-rewarded solution (20% saline, which is aversive to water-deprived crickets; Matsumoto & Mizunami 2006). The odors were always placed in the same container to account for the possibility that the plastic containers may absorb the odors, which may confuse the crickets as to what odor is in the container. A small plastic tube was also inserted above the cup where the cricket was placed into the maze. The tubing was connected to a vacuum, creating airflow that brought the odors closer to the cricket.

Olfactory and reversal learning

Crickets were divided randomly into two groups rewarded by a different odor, with half of them rewarded by vanilla, and half rewarded by strawberry. The side of the maze that the rewarding odor was on was switched following a pattern of LRRLRLLR wherein this example the container with the rewarded strawberry odor is on the left side, followed by a trial where the container with the non-rewarded vanilla odor is on the left and so on. This ensured that the cricket was not learning to associate the left or right side with the reward, but rather to associate the odor with the reward. This pseudo-random order also allowed for an equal number of trials to be done on both sides and prevented the same odor from appearing on the same side more than twice consecutively (Peréz et al. 2018, Abramson et al. 1988). Prior testing of 39 crickets revealed that there is no initial preference for one odor over the other, with crickets spending roughly equal time with both the vanilla odor and the strawberry odor sides (t-test, p=0.58).

During a trial, crickets had ten minutes to drink from either side and were free to travel to both sides of the maze until they drank from a dish, at which point the trial was stopped. If the cricket failed to drink from either side, then the trial was labeled as no choice and was not counted towards the learning criterion (see below), or to the learning speed of an individual. The time it took for a cricket to drink from a dish during a trial was put down as the ‘drink time’. These no choice trials were not included in the learning criterion as there was no way to know if the crickets did not choose to drink because they had not learned the association or if they were simply unmotivated to drink from the water dish for that trial. The learning criterion, the point where it was considered that the cricket had learned the association, was that the crickets had to choose the correct odor at least eight times within ten consecutive choices, corresponding to a chance binomial probability of about 5.5%. The number of trials until the learning criterion was met was the learning speed, with the learning speed being the last trial in the learning criterion.

After each trial, the container that the cricket visited was wiped clean with ethanol, and the tubing that the cricket went in was washed with soap and water before being cleaned with ethanol. The tubes were then dried before they were used again. Once the crickets learned the initial association, a reversal was performed in which the reward switched to the opposite odor. Once the cricket learned the association during the reversal (same learning criterion as for the initial learning), then the reward switched back to the original odor, for a total of one initial learning run, and two reversals. An individual cricket was tested until it had either 1: met the learning criterion for all of the reversals, 2: finished fifty trials within an experiment, including trials where it did not choose a side, without learning the association, or 3: had ten trials in a row where it did not move from its initial starting position. In either case two or case three above, the cricket was then considered to have not learned during that experiment.

Analysis

In order to make sure that the various behaviors that were measured varied consistently among individuals, and could thus be considered personality traits, repeatability tests were run on each of the behaviors using the R program rptR (Stoffel et al. 2017). The latency to emerge tests were Gaussian tests that had the average exit shelter time (the exit score) as the dependent variable, with the trial being a fixed effect and the ID of a cricket being a random factor. Neophobia was tested in a similar way, only with the average time it took for an individual to come into contact with the novel object being the dependent variable. For the aggression score, repeatability was calculated with the opponent’s aggression score as a fixed factor and the focal individual’s ID as a random variable. The learning speed was also tested for repeatability, which necessarily only included data from crickets that were considered to have learned by meeting the learning criterion (those that didn’t do not have a learning speed).

These tests were Poisson and were performed both with learning speeds in all three experiments (initial, first reversal, second reversal) and also for just the two reversal experiments, as initial learning and reversal learning are thought to involve different mechanisms (Dalley et al. 2004, Schoebaum et al. 2002). Lastly, a repeatability test on drinking time was done. The drink time was the average time it took for a cricket to drink from any petri dish during a trial across the entire experiment (i.e initial, first reversal, or second reversal). These were all fixed factors. The ID of the cricket was once again a random factor.

To obtain an overall aggression score for use as a predictor in models of learning speed, the raw aggression scores were put into a linear mixed effect model in R (Bates et al 2015) with the cricket's ID as a random factor and the opponent's aggression score as a fixed factor. I extracted the best linear unbiased predictors (BLUPs) from the model to obtain an aggression score for each individual that accounted for the variation in opponent behavior. The BLUP value for each individual was obtained by calculating an average value from 1000 simulations of the model using the arm package (Gelman & Su 2020) (following Dingemanse et al. 2020). While the use of BLUPS as fixed effects in statistical models does not account for uncertainty in their estimates (Hadfield et al. 2010, Houslay & Wilson 2017), alternative techniques result in biased estimates of the effect (Dingemnase et al. 2020), so I therefore used average BLUP values as the best representation of an individual's aggressiveness that accounts for variation in their experience due to their opponents' behavior. Afterwards a linear model was done to see if the aggression score was correlated to the exit score, with the exit score being the explanatory value and the aggression score being the dependent variable.

Separate binomial general linear models were run for each of the three experiments to see if any of the personality traits affected whether an individual met the learning criterion or not. There were two sets of models, one for aggression, and the other for sex and latency to exit.

However, for aggression, I only looked at effects on likelihood of learning in the initial learning experiment, because the latter two experiments had very small samples sizes (n=9 & n=6 respectively), and most of the individuals learned in both of those experiments. For the aggression model, whether an individual learned or not was the response variable, with the explanatory variables being aggression score, scaled drink time, and reward. The drink time was the average time it took for a cricket to drink, either from the reward (water) or the aversive stimulus (saline), across the trials. This variable was included because crickets who drank from a petri dish quickly would have had a shorter time between detecting an odor and getting either a reward or an aversive drink, increasing the likelihood that the cricket may have built a connection between the odor and the reward/aversive stimuli. This variable may also partially account for variation in motivation between individuals. I then tested whether sex, a scaled average latency to exit score, reward, or a scaled drink time affected whether or not an individual learned or not as the response variable. In this case, we were able to test these effects for each of the three experiments.

Two generalized linear mixed models (glmer) were tested to see if personality variables and other factors affected learning speed (modeled as a Poisson variable). The first model included the learning speed as the dependent variable and had the aggression score, the interaction between aggression score and experiment (i.e. initial, first reversal, or second reversal), the reward (strawberry or vanilla), and the average drink time as explanatory variables, and the cricket ID as a random factor. This model only included data from males due to the females not having a repeatable aggression score (see Results). For the second model, I tested whether learning speed was affected by sex, the scaled average latency to exit the shelter time, scaled drink time, reward, the interaction between latency to exit (the exit score) and experiment, and the interaction between sex and experiment. Cricket ID was included as a random factor. The time to approach the novel object was not included in the model because it was not found to be repeatable (see Results).

I did not run a model with both exit score and aggression score because of singularity issues. Interactions that were not significant were dropped from the final models. A Tukey post hoc test using the package emmeans (Length 2021) was used to make pairwise comparisons between learning speeds for the different experiments.

RESULTS

Repeatability of putative personality traits

The latency to come into contact with the novel object was not repeatable (R= 0, SE= 0.062, CI (0, 0.198), p= 1). However, the time it took to exit the shelter was repeatable (R= 0.547, SE= 0.074, CI (0.384, 0.675), p > 0.0001). Aggression score was found to be repeatable in males (R= 0.179, SE= 0.067, CI (0.053, 0.313), p= 0.002), but female aggression score was not repeatable (R=0.052, SE= 0.045, CI (0, 0.159), p= 0.154). Aggression was found not to have a significant relationship with latency to emerge (Est value = 0.026, Std Error= 0.483, t value= 0.055, p = 0.57).

Effects on whether individuals learned

Whether an individual actually learned or not was not affected by sex, aggression, and exit score (Tables 2-5). The rewarded odor also did not affect whether or not an individual learned or not (Tables 2-5). The time it took for an individual to drink did have significant effects on whether individuals learned, with individuals with faster drink times more likely to learn, but only for the initial learning experiment in the sex and exit score model. In the first and second reversals, drink time did not have a significant effect on whether or not an individual learned (Tables 2-4).

Effects on learning speed

A total of twenty-four individuals met the learning criteria at least once out of fifty-four individuals tested (Table 6). Learning speed across all three experiments was not repeatable (R= 0.002, SE= 0.106, CI (0, 0.367), p= 0.497). There was also no significant repeatability of learning speed when I examined only the two reversal experiments (R=0, SE= 0.174, CI (0, 0.571), p= 0.5). However, the drink time was found to be repeatable (R= 0.738, SE= 0.094, CI (0.522, 0.876), p> 0.0001).

Aggression did not have a significant effect on learning speed (Table 7 and Fig 3). The interaction between aggression score and learning trial was not significant and dropped from the final model. The only significant factor affecting learning speed in the aggression model was the relationship between learning speed in the initial learning experiment and the learning speed of the second reversal, with individuals who learned faster in the initial learning experiment learning faster in the second reversal (Table 7).

For tests of the effect of latency to exit on learning speed, the interaction between latency to exit and experiment was not significant and dropped from the final model. Individuals that had a higher exit score learned significantly faster than individuals with a lower exit score (Table 8 & Fig 4). There was a significant interaction between sex and experiment (Table 8), with males learning faster in the initial and first reversal, but learning slower than females in the second reversal (Fig 5). Individuals that had a faster initial learning speed had a faster first reversal learning speed, but there was no relationship between initial learning speed and the second reversal speed (Fig 6). The reward type and the drink time had no significant relationship with learning speed.

The Tukey post hoc test showed that there was a significant difference between learning speeds for the initial learning and the first reversal (see table 9 and figure 5) and between initial learning and the second reversal (table 9), with the crickets as a whole learning faster in the initial learning experiment. However, there was no significant difference in learning speed between the first and second reversals (table 9 and Fig 5).

DISCUSSION

Acheta domesticus was capable of olfactory learning, and reversal learning, with around half of the individuals tested meeting the learning criterion in the initial learning experiment. This corresponds with results from crickets in the genus *Gryllus*, where olfactory learning and reversal learning was demonstrated (Matsumoto & Mizunami 2000, Matsumoto & Mizunami 2002, Sugimachi et al. 2016). The time it took for an individual to leave a shelter was repeatable and related to individual learning speed, but aggression, although repeatable, was not related to learning speed. Learning speed also was affected by an interaction between sex and experiment, with males learning faster in the initial and first reversal, and females learning faster in the second reversal. Although the overall repeatability of learning speed across the three experiments was not significant, there was a significant positive correlation between learning speed in the initial learning period and the first reversal, but not between learning speed in either of those experiments and learning speed in the second reversal.

Repeatability of Learning

Reversal learning is thought to involve additional processes in comparison to initial associative learning (Dalley et al. 2004, Schoenbaum et al. 2002). Due to these differences in brain regions, initial associative learning ability is not necessarily expected to correlate with reversal learning ability (Bebus et al. 2016, Guenther et al. 2014).

This difference between the two forms of learning may be one reason why there was no significant repeatability in learning speed across my three experiments. This can be seen in great tits, *Parus major,* where learning speed was not repeatable between the initial learning and the later reversals (Reichert et al. 2020). In the same study, it was found that there was no repeatability in reversal learning speed for the blue tit, *Cyanistes caeruleus* (Reichert et al. 2020), which is similar to the results in this study. A meta-analysis by Cauchoix et al. (2018) found that reversal learning performance in general was not very repeatable.

Although there was no overall repeatability for learning speed, in the mixed model analysis I found that there was a significant positive relationship between learning speed for the initial learning and learning speed in the first reversal, suggesting that at least for these two experiments individuals were consistent in their behavior. That means that the individuals who learned fastest in the initial learning experiment also learned fastest in the first reversal learning experiment. This contrasts with expectations for no repeatability between initial and reversal performance based on a hypothesized difference in the mechanisms involved. There was a similar finding for color discrimination in pheasants, in which individuals that more quickly associated a color cue with a reward were also faster in the reversal when the reward was associated with the opposite color (Van Horik et al. 2019). However, when the experiment was repeated with a second color pair, there was only a weak positive association between the initial learning and the first reversal learning speeds (Van Horik et al. 2019). In one study one bumblebees, *Bombus terrestrisinitial*, associative learning performance is positively correlated with a faster learning speed in later reversals (Raine & Chittka 2012). However, several other studies showed that learning quickly in associative learning is negatively correlated with a faster reversal learning speed, suggesting a trade-off between the two (Guenther et al. 2014, Jones et al 2020, Bebus et al. 2016).

One potential explanation for the finding of a positive correlation between initial learning speed and the first reversal learning speed is that the individuals who learned faster may have been more motivated, in terms of thirst level or willingness to explore the arena. Motivation is known to affect performance and the likelihood of learning (Van Horik et al. 2017, Rowe & Healy 2014), and likely played some role in variation in performance in this study. These motivational effects may have carried over from the initial to the first reversal, but perhaps not to the second reversal because by this time only the most motivated crickets were left (i.e. these were the only ones that met the previous learning criteria, refer back to Table 2).

I attempted to control for motivation by making sure that all the crickets were deprived of water for twenty-four hours, though food and water deprivation does not always affect all individuals equally (Rowe & Healy 2014). I also attempted to account for motivation with the drink time variable (the average amount of time it took for a cricket to drink from the water in a trial after being released). Drink time may reflect individual motivation to drink, with individuals who drank quicker being more motivated to get to the water than the individuals who waited to drink towards the end of the trial, although it may also reflect non-motivational factors such as exploratory tendency. Indeed, I found that drink time had a significant effect on whether or not an individual learned, with individuals with faster drink times more likely to meet the learning criterion, so it could be that only the individuals that were sufficiently motivated made it past the initial learning experiment. This would be a similar result to Chow et al., who found that gray squirrels, *Sciurus carolinensis*, that spent more time with a puzzle apparatus solved it faster than individuals that spent less time with the apparatus (2016). Another study testing *Phasianus colchicus* chicks found that the birds that approached the test apparatus the fastest, and the birds that made the most attempts were the most likely to succeed in a problem-solving test (Van Horik & Madden 2016).

Another thing to note is that a little than half of the crickets actually learned. One reason for this lack of learning in half of them could be that the crickets' ecology does not require them to do a lot of olfactory learning. An example of an insect being constrained due to its ecology can be seen in honeybees, with a subspecies, *Apis mellifera syriaca,* being worse at reversal learning compared to another subspecies, *Apis mellifera caucasica,* due to *A. mellifera syrica* specializing on fewer flowers in the wild (Perèz Claudio et al. 2018). Other research has also shown that crickets have trouble learning in shuttle boxes (Stauch In Press), whereas honey bees have been shown to learn in shuttle boxes (Dinges et al. 2013, Peréz Claudio et al. 2018).

Learning speed in the first reversal was not correlated to the learning speed in the second reversal. This is somewhat surprising as one might think that the two reversals may involve more similar learning processes than the initial and the first reversal, which has been shown to be the case in great tits, *Parus major (*Reichert et al. 2020). One possibility could be that after the first reversal experiment other learning processes began to affect individuals. For instance, after the first reversal learning experiment, serial reversal learning begins to occur. Serial reversal learning consists of switching which choice gives an individual a positive stimulus and which one does not multiple times (Liu et al. 2016). This may in essence lead to animals 'learning to learn' by being better able to predict what to do once a reversal occurs. In common marmosets, *Callithrix jacchus,* the part of the brain that does higher order processing that is needed for rule-based strategies that would allow an individual to perform better in serial reversal learning is different from the part of the brain that is most heavily involved in learning during the first reversal (Rygula et al. 2010). It could also be that the crickets began to generalize their choice to both odors; this has been shown to occur in both honey bees (*Apis mellifera*) and bumblebees (*Bombus impatiens*), whereas the reversals go on the insects began to generalize the association between reward and both stimuli because of their past experiences making their decisions less accurate (Mota & Giurfa 2010, Sherry & Strang 2015).

Personality effects on learning

Aggression score did not predict whether or not an individual learned, and it also did not have a significant effect on learning speed. The lack of a significant effect may have been because the sample size was too small to detect any effect, particularly because of the small sample size for the later reversals. It may be that aggression simply is not strongly related to learning speed. Previous studies have found mixed results on the relationship between aggression and learning. In one species of ants, *Camponotus aethiops,* aggression plays little role in learning (Udino 2017). In contrast, in rodents such as *Myodes glareolus* and *Cavia aperea*, aggression is indeed related to learning, with more aggressive individuals being faster at associative learning and slower at reversal learning (Guenther et al. 2014, Mazza et al. 2018). Related to this is the possibility that aggression does not play a role in olfactory associative and reversal learning, but it may still affect performance in other learning tasks. For example, in some species, less dominant individuals are better at innovative problem solving (Laland & Reader 1999, Cole & Quinn 2012).

It could also be that the aggression score was not an accurate representation of a cricket's aggression level. While the aggression scores were repeatable for males and the BLUP method used results in unbiased measures of the trait after controlling for confounding effects (Dingemanse et al. 2020), aggression is a complex group of behaviors, and the expression of aggression is highly context-dependent, in particular with respect to the behavior of the opponent (Briffa 2008). Aggression was also not correlated with latency to emerge among the crickets, which could lead to aggression not playing an important role in the proactive/reactive axis in crickets. Another study on *Acheta domesticus* also found no correlation between latency to emerge and aggressive behavior, though they latency to emerge was correlated with other behaviors such as calling behavior and anti-predator behavior (Wilson et al. 2010).

In contrast, the latency to exit was both repeatable and a significant predictor of learning speed: individuals who exited the shelter more quickly had a slower learning speed than the individuals who took a long time to exit the shelter. However, the exit shelter score was not a good predictor in determining if an individual learned in the first place. Other studies that have looked at the proactive and reactive axis have found that variation along this axis does not necessarily predict whether an individual learns, but rather affects how fast an individual learns (Guenther et al. 2014, Mazza et al. 2018), which is consistent with my findings.

However, in general, my results do not support the prediction that more proactive individuals do better at initial learning and worse at reversal learning compared to more reactive individuals (Sih & Del Giduce 2012), because there was no interaction between latency to exit and experiment. Instead, there was a main effect of latency to exit, suggesting a similar effect across the three experiments. This is in contrast with numerous other studies that found a strong association between proactive traits and initial learning speed, with more proactive individuals learning more quickly (Dugatkin & Alfieri 2003, Guillette et al. 2009, Bensky et al. 2017). One would expect that the individuals that exited the shelter earlier would come into contact with the reward before the individuals who stayed in the shelter longer and would thus have a faster initial learning speed than individuals who exited the shelter later. That said, several studies have also found that proactive individuals are not better at initial learning than more reactive individuals (Sommer-Trembo & Plath 2018, Mesquita et al. 2015). I did find some evidence that more reactive individuals may be more flexible learners and do better at reversals, though the more reactive individuals performed better at all the learning experiments. More reactive individuals have been found to do better in many reversal experiments (Guenther et al. 2014, Mazza et al. 2018, Bebus et al. 2016).

One reason that the crickets that exited the shelter more quickly were slower learners could be because the trial arena was a y-maze, perhaps resulting in some elements of spatial learning being involved in the learning task. In some species, more proactive individuals do worse in spatial learning tasks (Bousquet et al. 2015, White et al. 2017). Another possibility could be that the time to exit shelter is not part of the proactive/reactive axis. This might be because other factors such as motivation may have played a more important role in determining when an individual left the shelter. Even exploratory behaviors, which are widely believed to fall on the more proactive side of the proactive/reactive axis, can have different results that are not repeatable, which can make determining what behaviors fall under the proactive/reactive axis complicated (Dochtermann & Nelson 2014).

Sex and Learning

There have been numerous reviews that look at the major factors that explain individual variation in learning (Boogert et al. 2018, Rowe & Healy 2014), but sex is often left out or not discussed in detail. I found that there was an interaction between sex and learning experiment on learning speed. Females learned faster in the first reversal compared to both the initial and the second reversal, while male crickets were fastest in the initial, but seemed to learn more slowly for each subsequent reversal. Males were also faster learners than females in the initial and first reversal experiments, while females were faster than males in the second reversal experiment. It could have been that male crickets were more proactive than female crickets, and this behavioral difference was responsible for the difference in learning speeds, but there was no significant difference in exit scores between the sexes (Est Values = -3.822, Std Error= 90.120, p= 0.967). However, the average aggression score for males from all aggression scores though was far higher (78.374) compared to the average aggression score for females in all trials (3.061), although at least within males’ aggression score was not related to learning speed.

Another possible explanation for these sex differences could be that female crickets were better at serial reversal learning, due to the different sexes learning in different ways or being different in specific components of the learning task. For example, in guppies and macaques, females are better than males at reversal learning tasks (Ha et al. 2011, Petrazzini et al. 2017), and among honeybees females are better at aversive learning than males are (Dinges et al. 2013). In contrast, in mollies, males are better than females at reversal learning (Fuss & Witte 2019).

Conclusions

Our study found a relationship between some components of animal personality and learning speed. Although the direction of that influence does not fully correspond with the hypothesized speed versus flexibility trade-off (Sih & Del Giduce 2012), it does show that animal personality can explain some of the variations in learning among individuals. The overall effect of animal personality on learning remains in question, with a recent meta-analysis showing that while personality affects learning, the directionality of these effects, and which personality traits are associated with better performance, is highly variable across species (Dougherty & Guillette 2018). Thus, more work is needed to parse out the exact relationship between personality traits and learning to better understand why individual variation in learning exists, and whether this individual variation is under selection due to its consequences for individual fitness (Boogert et al. 2018).

TABLES AND FIGURES

Table 1.1 – Weighting of aggressive behaviors to calculate aggression scores

Behavior	Description	Weight
Antennal fencing	Crickets rapidly antennae the other’s antennae	1
Rock Body	Stationary cricket rocks body rapidly back and forth	1
Kick	Kicks leg towards conspecific	2
Threat posture	Raise itself on its forelegs	2
Mandible flare	Cricket hyperextends mandibles	3
Chase	Runs after conspecific	3
Bite	Pinches conspecific with mandibles	3
Lunge	Rushes conspecific with open mandibles	3
Grapple	Crickets butt heads and/or interlock mandibles and push	4

The aggression values for different behaviors that were observed during the aggression trials. Each behavior would be multiplied by the total time that the individual spent performing the behavior.

Table 1.2 Effects on whether an individual learned in the initial learning experiment

Variable	Estimated value	Standard error	z-value	p-value
Latency to exit	0.254	0.335	0.758	0.448
Sex (Male)	-1.332	0.683	-1.950	0.051
Reward (Vanilla)	0.641	0.654	0.981	0.327
Drink time	-0.710	0.340	-2.090	0.037

Results of a binomial GLM that tested for relationships between whether an individual met the learning criterion or not in the initial learning experiment and the latency to exit, sex (reference was female), odor of the reward (strawberry as the reference), and the drink time.

Table 1.3 Effects on whether an individual learned in the first reversal experiment

Variable	Estimated values	Standard error	z-value	p-value
Exit Score	-1.158	0.912	-1.270	0.204
Sex (Male)	-2.693	2.875	-0.937	0.349
Reward (Vanilla)	22.274	4906.202	0.005	0.996
Drink time	-3.142	1.958	-1.605	0.109

Results of a binomial GLM that tested for relationships between whether a cricket learned or not in the first reversal learning experiment and the latency to exit, sex (reference was females), odor of the reward (strawberry as the reference), and the drink time.

Table 1.4 Effects on whether an individual learned in the second reversal learning experiment

Variable	Estimated values	Standard error	z-value	p-value
Exit Score	0.589	0.710	0.830	0.407
Sex (Male)	1.788	1.602	1.116	0.264
Reward (Vanilla)	1.372	1.342	1.023	0.307
Drink time	0.387	0.681	0.568	0.570

Results of a binomial GLM that tested for relationships between whether a cricket learned or not in the second reversal learning experiment and the latency to exit, sex (reference was females), the odor of the reward (strawberry as the reference), and the drink time.

Table 1.5 Effects of aggression on learning in the initial learning experiment

Variable	Estimated values	Standard error	z-value	p-value
Drink time	-0.715	0.513	-1.393	0.164
Reward (Vanilla)	0.693	1.040	0.667	0.505
Aggression score	-0.459	0.288	-1.594	0.111

Results of binomial GLM that tested for relationships between whether a cricket learned or not in the initial learning experiment and the drink time, the aggression score, and the odor of the reward (strawberry as the reference).

Table 1.6 Proportion of crickets that learned in each experiment.

	Initial	1st Reversal	2nd Reversal
Male	9/24 (38%)	6/9 (67%)	5/6 (83%)
Female	15/26 (58%)	11/14 (79%)	7/11 (64%)
Total	24/50 (48%)	17/23 (74%)	12/17 (71%)

Each cell shows how many crickets met the learning criterion as a proportion of how many were tested. Only individuals that met the learning criterion in the previous experiment continued to be tested in the subsequent experiment. Note that one female died between the initial and the first reversal so only fourteen females were tested for the first reversal.

Table 1.7 Relationship between learning speed and aggression

Variable	Estimated values	Standard error	z-value	p-value
Drink time	-0.074	0.078	-0.948	0.343
Aggression Score	0.115	0.069	1.665	0.096
Reward (vanilla)	-0.080	0.120	-0.662	0.508
Experiment (Reversal 1)	0.272	0.149	1.826	0.068
Experiment (Reversal 2)	0.734	0.136	5.402	< 0.0001

Results from a Poisson GLMM that tested the relationship between learning speed and aggression score, drink time (the average time it took for a cricket to drink during a learning experiment), the stimulus used as the reward and experiment (initial, 1st reversal, 2nd reversal). The reference level for the experiment is the initial learning period. The reference level for the reward stimulus was strawberry. This table shows results for males only because females did not have repeatable aggressive behavior.

Table 1.8 Relationship between learning speed, sex, and latency to exit

Variable	Estimated values	Standard error	z-value	p-value
Latency to exit	-0.109	0.051	-2.135	0.033
Sex (Male)	-0.338	0.139	-2.436	0.015
Reward (Vanilla)	-0.124	0.073	-1.710	0.087
Drink time	-0.091	0.054	-1.708	0.088
Experiment (Reversal 1)	0.293	0.100	2.942	0.003
Experiment (Reversal 2)	-0.082	0.127	-0.645	0.519
Sex(M) * Reversal 1	-0.082	0.178	-0.460	0.646
Sex (M) * Reversal 2	0.765	0.188	4.064	< 0.0001

Results from a Poisson GLMM that tested the relationship between learning speed, sex, exit score ("Latency to exit"), drink time (the average time it took for a cricket to drink during a learning experiment), the stimulus used as the reward and experiment (initial, 1st reversal, 2nd reversal), and the interactions between sex and each learning experiment. The reference level for the experiment is the initial learning period. The reference level for the reward was strawberry. The reference level for sex is female.

Table 1.9 Comparisons of learning speed in the three experiments

Comparison	Estimated value	Standard error	z-ratio	p-value
Initial - First Reversal	-0.297	0.074	-4.009	.0002
Initial - Second Reversal	-0.228	0.083	-2.753	.016
First Reversal - Second Reversal	0.069	0.079	0.880	.653

Shows the results of the Tukey post hoc test that compares the learning speed from each combination of the three learning experiments (initial, the first reversal, and the second reversal).

Table 1.10 Hypotheses and results

Hypothesis	Results
More aggressive individuals would correlate to faster initial learning speed, but slower reversal learning speed.	Aggression had no significant effect on learning speed. Aggression also only qualified as a personality trait in males, not females.
Individuals that exited the shelter earlier would have a faster learning speed but would be slower at the reversal learning speed.	Individuals that exited the shelter earlier were slower learners at all stages of learning, whether it was during the initial learning experiment or one of the reversals.
Individuals that came into contact with a novel object earlier would have a faster learning speed but would be slower at the reversal learning speed.	Coming into contact with a novel object did not make the criteria for being a personality trait.

This table shows the results from the various parts of my initial hypothesis, there is nothing related to sex here, as I did not make an initial hypothesis regarding the effects that sex would have on the crickets.

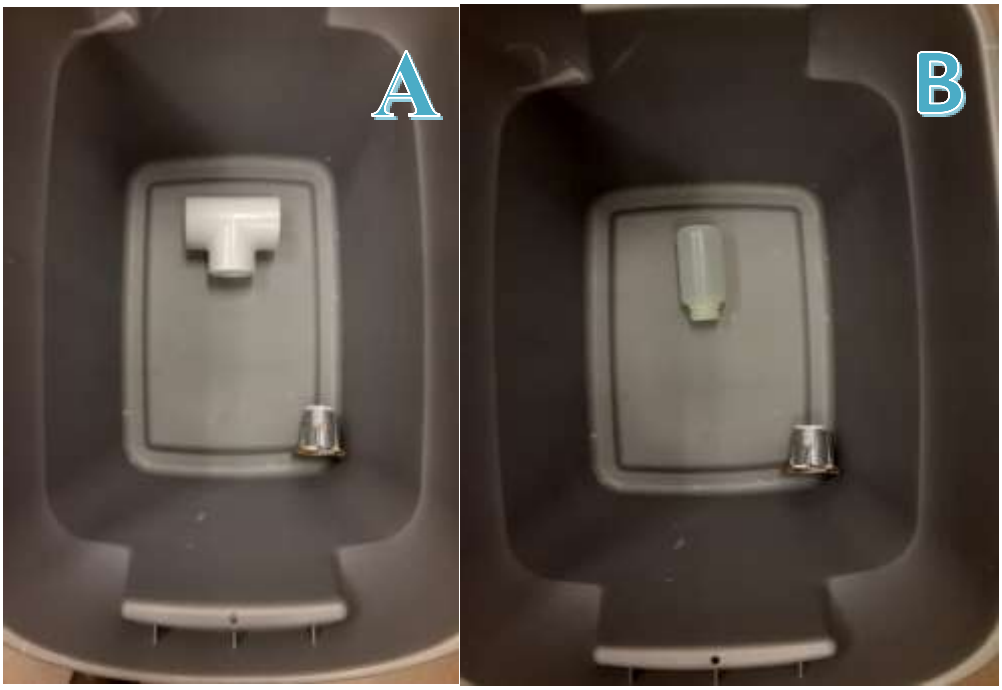

Figure 1.1**-** Neophobia trial arenas. This shows what the basic setup for the neophobia trials looked like, with the novel object towards the end of the container and the shelter in the righthand corner facing the object. The images show the objects for trial one (A) and for trial two (B).

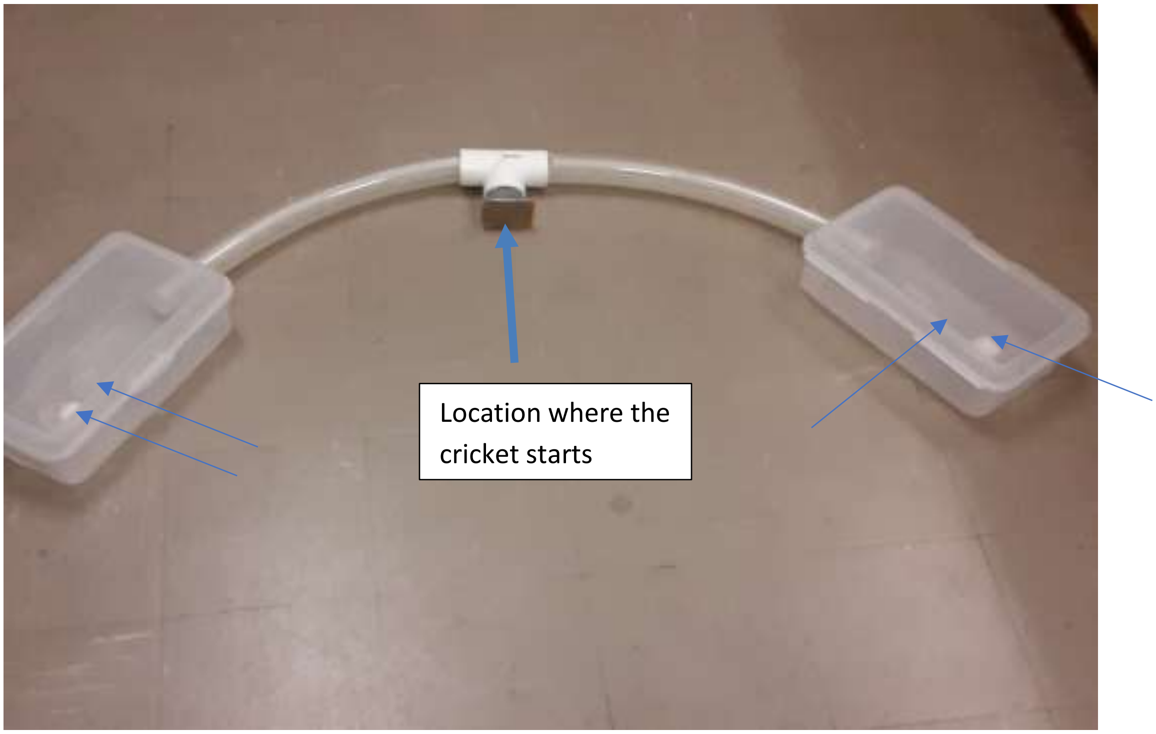

Figure 1.2**-** The setup for the olfactory and reversal learning tests. The petri dishes were filled with either regular water or a 20% saline solution. Each container will contain two petri dishes, one with water and the other with a cotton ball container an odor. The side that each odor is on will vary with the tests to prevent positional bias. The smaller arrows in the picture point to the location of the petri dish with water and the petri dish that holds the cotton ball. The larger arrow shows the location where the cricket starts.

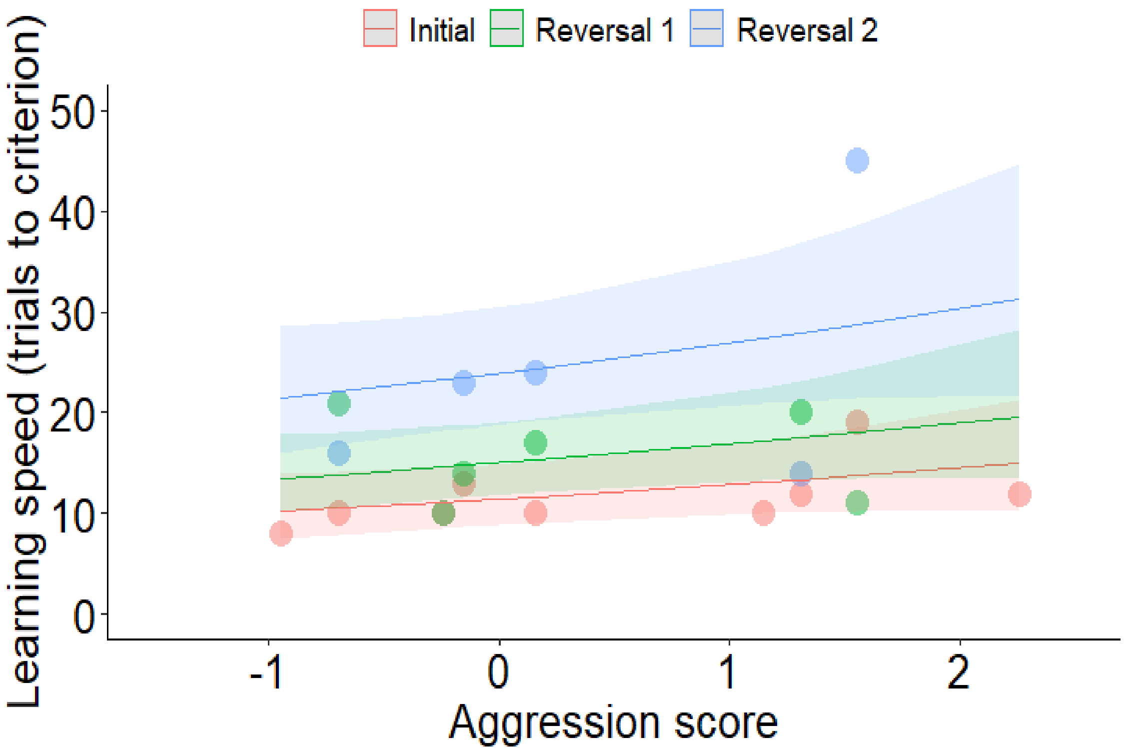

Figure 1.3- Shows how aggression scores were related to learning speed for males that learned. The data points represent raw BLUP scores, the higher the score the more aggressive the individual was after accounting for all other variables, and the lower aggression scores were lower when accounting for all possible other variables. The shaded area is the 95% confidence interval.

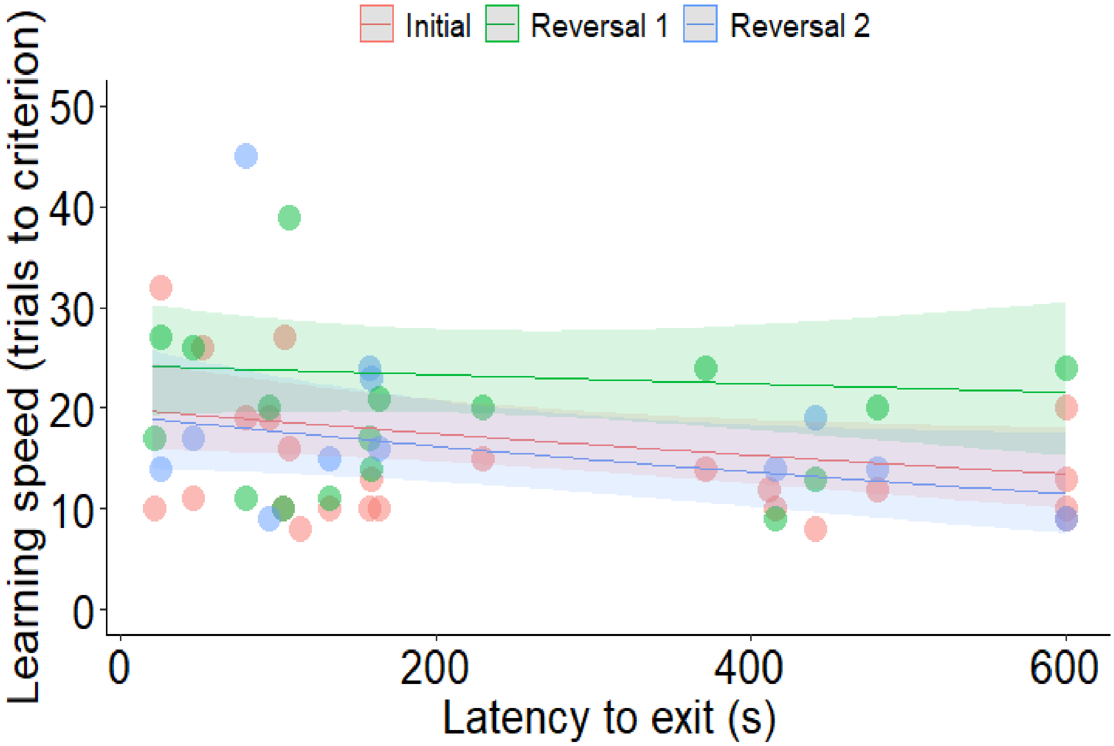

Figure 1.4- Relationship between latency to exit ('exit score') and learning speed. The exit score was the average time that it took for an individual to exit the shelter in the two neophobia tests. A higher score meant that it took longer for the cricket to leave the shelter. Learning speed was significantly affected by the exit score, with individuals with a higher exit score having a faster learning speed (fewer trials to criterion). The individual points represent the raw data and line represents the estimated marginal means. The shaded area is the 95% confidence interval.

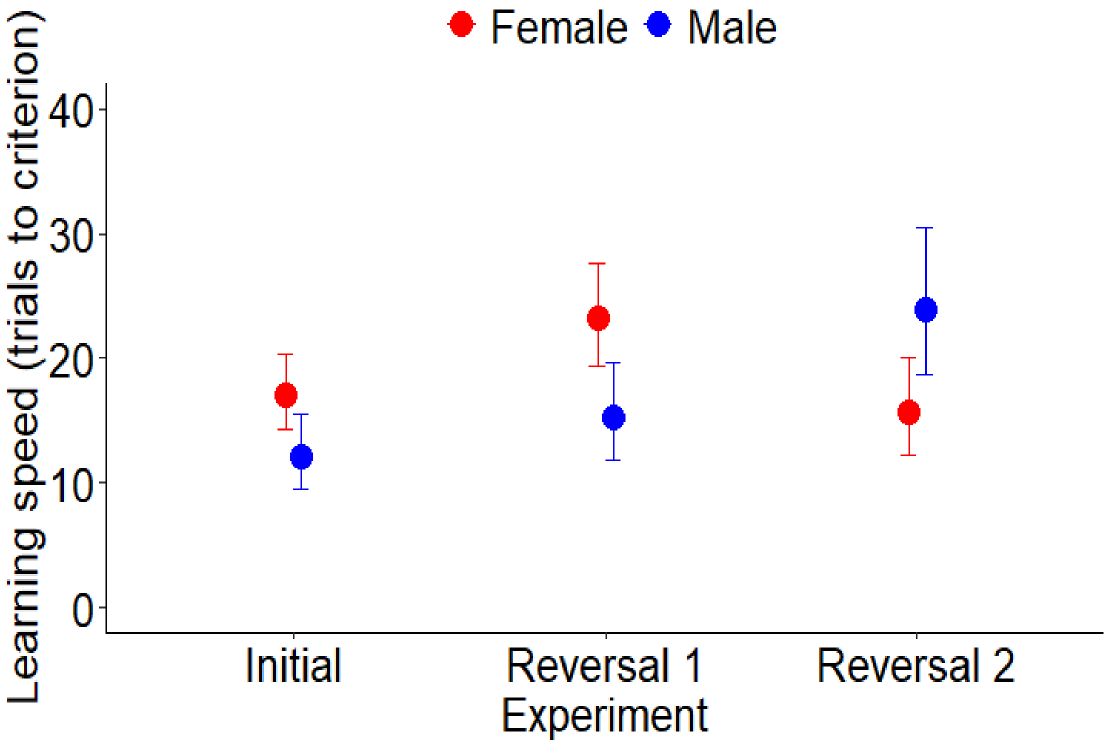

Figure 1.5- Learning speed for each experiment for males (red) and females (blue). Dots correspond to estimated marginal means (± 95% confidence interval) from a generalized linear mixed model of effects on learning speed (Table 8). Learning speed was quantified as the number of trials it took for an individual to meet the learning criterion (successfully drinking from the reward in a moving window of eight out of ten trials), so smaller values equal faster learning. Females were slower on the first two learning experiments but were faster in the second reversal.

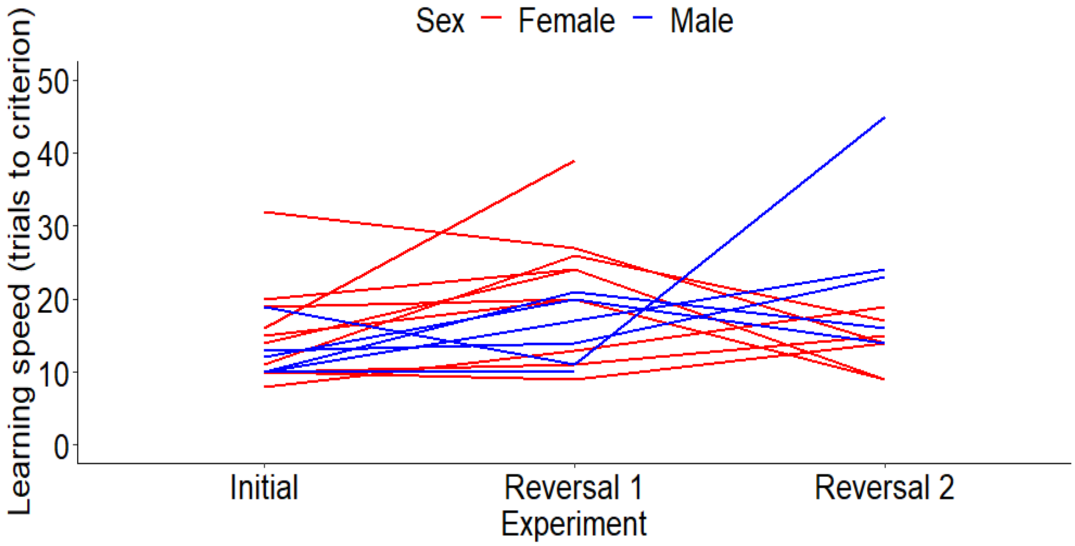

Figure 1.6- Individual variation in learning speeds across the three experiments. Each line represents the performance of a single individual. Only individuals that met the learning criterion in both the initial and first reversal experiments are depicted. Individuals that were faster in the initial learning experiment were generally also faster in the first reversal, but there is no consistent association between an individual's learning speed in the first reversal and its learning speed in the second reversal.

CHAPTER II

ACHETA DOMESTICUS AND THE POTENTIAL FOR SOCIAL LEARNING

INTRODUCTION

Other individuals can often be a valuable source of knowledge about the environment, and even about other members of the social group because they are a source of ‘public information’. Public information is the cues and signals made by an individual that are available to other individuals, and that can be used to gain more information on the social or physical environment (Goodale et al. 2010). Social learning is a form of learning that involves changing behavior in a novel way based on the actions of a conspecific, and it often uses public information (Whiten & Ham 1992). It can play an important role in cognitive studies, with cognition being the neuronal processes associated with acquiring, storing, and using information (Dukas 2004).

Social learning has been documented in a wide variety of organisms, ranging from crickets (Ebina & Mizunami 2020) and other invertebrates (Webster & Fioritio 2001) to various vertebrates such as guppies (Chapman et al 2008), dolphins (Kuczaj II et al. 2012), birds (Slagsvold & Wiebe 2011), and bearded dragons (Kis et al 2015). Social learning can increase fitness (Grüter & Leadbeater 2014). For example, in fairy-wrens, individuals can learn to attend to heterospecific alarm calls to avoid predators (Magrath et al. 2015, Fallow et al. 2013), and in many songbird species, younger birds are taught songs by a tutor, increasing both individuals’ survival rates (Beecher et al. 2020).

Mechanisms of social learning range from individuals simply making use of public information that they received through observations (Danchin et al. 2004), imitations of other animals (Heyes 1994), and to learning the information through teaching (Thornton & Raihani 2010).

However, individual animals do not always make use of public information, and individuals have also been shown to vary in their use of public information and the likelihood and ability to socially learn from others (Cadieu et al. 2010, Aplin et al. 2013). There are several explanations for variation in social learning. One reason is that no experienced individuals are present in the social environment. In some species, individuals will only attend to certain experienced individuals and may disregard information provided by less experienced individuals (Barett et al. 2017). Alarm calls are a good example of this, as adults tend not to react to juvenile alarm calls as strongly as they do to those of other adults (Hollén & Radford 2009).

There are also trade-offs between the use of public information and an individual’s own information gathering. For instance, in great tits, *Parus major*, individuals often chose to remain near their social mate, even if this prevented them from accessing good foraging sites (Firth et al. 2015). Social learning might also be less likely if an individual is too aggressive towards other individuals and drives them off before socially learned information can be obtained (Cadieu et al. 2010).

Personality and Social Learning

Animal personality is the consistent inter-individual differences in behavior across time (Réale et al. 2007). Personality may play a role in whether or not an individual socially learns. For instance, personality may affect the number and strength of an individual’s social relationships (Aplin et al. 2014), and there is some evidence that more proactive individuals have many weaker relationships, and more reactive individuals have fewer, but stronger, relationships (Aplin et al. 2013).

These differences in social interactions could therefore affect the opportunity for social learning, and also how likely an individual may be to actually use the social information that it gathers from others (Smit & van Oers 2019). This difference between personality types could result in different social learning strategies, with more reactive individuals favoring public information over private information, and more proactive individuals doing the opposite. For instance, it could be that more reactive individuals are more willing to use social information because they generally have stronger relationships (Aplin et al. 2013), as is the case with geese (Kurvers et al. 2010). This can also be seen in guppies, where more proactive individuals would forgo the use of public information if they had private information that conflicted with it, while in contrast, more reactive individuals were more likely to use public information when it conflicted with private information (Trompf & Brown 2014).

How aggression can influence social learning

Social learning might be impacted by aggression if more aggressive individuals are less sociable, and therefore have fewer opportunities to socially learn (e.g. orangutans, Schuppli et al. 2017). Aggression could also affect who an individual may socially learn from. For example, in the Atlantic Canary, *Serinus canaria*, males did not socially learn from each other due to displaying aggressive behaviors to each other, but the males were capable of social learning from females (Cadieu et al. 2010). The effects of aggression on social learning may also be indirect. Living in a dense population has been shown in some cases to raise aggression levels in several species (Hoelzer 1987), and population density, in turn, can affect social learning abilities (Chapman et al. 2008). More aggressive individuals have also been shown to disperse greater distances than less aggressive individuals (Michelangeli et al. 2017, Duckworth & Badyaev 2007), which would limit their chances to interact with and learn from conspecifics.

An alternative hypothesis is that more aggressive individuals may be better at social learning because they pay more attention to subordinate individuals when there is an opportunity to exploit them for resources as in the scrounger/producer game (Liker & Barta 2014). Aggression is also not always correlated with low sociability (Scott et al. 2018), especially if the more aggressive individual is more dominant, making them more central to the social network and more likely to potentially observe others and exhibit social learning (Jones et al. 2017). More work is therefore needed on this subject to determine whether and how aggression affects social learning.

How neophobia can influence social learning.

Neophobia, or the aversion to novelty (Greggor et al. 2015), is also likely to be related to social learning. One hypothesis is that less neophobic individuals will be less likely to use social information, as they will be more likely to interact with new objects in their environment, lessening the likelihood that they first observe others interacting with the object before they do so themselves, as well as reducing the need to learn from others about the object (Kurvers et al. 2010). This would fit with the prediction that more reactive individuals (which tend to be more neophobic) rely more on public information gained from other individuals, while more proactive individuals (which tend to be less neophobic) rely more on their own information (Trompf & Brown 2014). On the other hand, low levels of neophobia are positively related to social learning ability in pigeons (Bouchard et al. 2007). This could potentially be because the less neophobic individuals also were more observant of others and were then more willing to approach and handle novel objects that they saw other conspecifics use.

Insects and Social Learning

Some insect species have the ability to socially learn (Webster & Fioritio 2001), although most research has been focused on eusocial species. One of the most well-known cases of social learning in insects involves the honey bee, which does a waggle dance to describe the location of a potential food source to conspecifics (Frisch 1967), though research has since shown that individuals often ignore the information depending on private information instead (Grüter et al. 2008, Grüter & Ratnieks 2011). Bumblebees, *Bombus terrestris*, have also shown some form of social learning, with individuals switching to more productive flowers faster when they are in a presence of an experienced forager versus when the individual is by itself (Leadbeater & Chittka 2007).

Non-eusocial insects have also been shown to socially learn, for instance, female fruit flies, *Drosophila melanogaster*, have been shown to choose male fruit flies based on other females' preferences (Sarin & Dukas 2009). Fruit flies have also been shown to have a preference for choosing oviposition sites on media that other individuals had already been observed to choose (Battesti et al. 2012). Some cricket species might also be able to socially learn. Wood crickets, *Nemobius sylvestris*, observing crickets have been shown to follow social cues from demonstrators with regards to anit-predator behavior, and would continue to show the behavior after the demonstrators were removed from the observers' presence (Coolen et al. 2005). *Gryllus bimaculatus* have also been shown to learn from conspecifics about the location of a water reward when the water dish was paired with a particular odor (Ebina & Mizunami 2020).

Hypothesis

Here, I investigate social learning and its relationships with personality in female *Acheta domesticus.* To do this I attempted to train focal female crickets to associate a reward (water) with a particular odor by observing a demonstrator cricket that had been brushed with that odor and trained to approach the water. After this training, I tested for social learning by examining whether the focal cricket showed a preference for the demonstrator's odor over a different odor in a series of test trials. I hypothesize that personality traits will have an impact on whether individuals socially learn. I predict that individuals who display more aggressive behavior will be less likely to socially learn because individuals who display aggressive behaviors more often will chase away demonstrators and will not have the opportunity to learn. I also predict that higher levels of neophobia will be associated with greater social learning because more neophobic individuals will be more reliant on information from conspecifics than less neophobic individuals, who are more capable of gathering their own information in the novel experimental setup. I also predict that there will be a positive correlation between the amount of time an individual spends near a conspecific during the experiment and whether or not it socially learns.

METHODS

The crickets used for the social learning experiment were female *A. domesticus* purchased at six weeks of age from Fluker's Farms (Port Allen, LA). Females were housed individually in the same containers that were used for the olfactory learning experiments and had a similar maintenance schedule (see Chapter I). Prior to the social learning tests, all of the focal female crickets were tested in neophobia trials that were identical to the ones that were used for the olfactory learning experiment (See Chapter I).

The learning apparatus

The social learning experiment took place in a y-like maze made out of transparent acrylic plexiglass. The dimensions of the maze were 45.7 cm wide and 61 cm long (see figure 7 for an image of the maze). A blank white paper was placed around the maze to limit the crickets from learning any landmarks outside of the maze.

The social learning training trials

To test for social learning, I paired a ‘demonstrator’ cricket that had been trained to move to the water dish in the maze, with a naïve ‘focal’ cricket. To train the demonstrator crickets, I deprived them of water for 24 hours and then placed them in the maze, in which a petri dish of water was placed on one side of the ‘Y’. Note that no odors were used during the training of demonstrators; the aim was to familiarize the demonstrator with the maze, and for the demonstrator to learn to find the water in the maze. I trained each individual in two ten-minute trials and required them to drink from the water at least once per trial to be used as a demonstrator.

The social learning trials consisted of two parts, eight training trials, and up to six test trials. During the training trials, the demonstrator cricket was placed in the maze with the focal cricket (n = 32). Some demonstrator crickets were used for more than one focal cricket, but they were only the demonstrator for one focal cricket per day. The focal cricket was naïve to the maze, while the demonstrator cricket had prior experience in the maze. Both crickets were deprived of water twenty-four hours prior to the beginning of the trial. Before the training trials began, the demonstrator cricket was brushed six times with 0.25 ml of either a vanilla extract or a strawberry extract using a q-tip. The extract was reapplied to the demonstrator every half-hour for the duration of the training trials. The aim was to test whether the focal cricket would learn to associate the odor that was applied to the demonstrator cricket with the reward of water that the demonstrator would go to in the maze.

In each training trial, the focal and the demonstrator crickets were placed in the maze underneath separate plastic cups for two minutes, whereupon the cups were picked up and the crickets were free to roam the maze. In one arm of the maze was a petri dish filled with water. The arm where the water was located was switched on an LRRLRLLR order, where the water would be on the left side of the arm followed by two trials where the water would be located on the right side before switching back to the left side. This was done to prevent a side bias from developing. Behind the water dish, there was another petri dish with a cotton ball that had no extract placed on it, to familiarize the crickets with these objects that would also be present in the test trials.

A training trial ended either when the focal cricket drank from the petri dish or after ten minutes. During the training trials, the time that the two crickets spent within an antennae's length apart from each other were recorded, as was the frequency and duration of aggressive behaviors. The aggression behaviors were recorded in the same way they were recorded in Chapter 1. All recording was done with a Sony DCR-SR85 handycam. All behaviors were analyzed using Boris (Friard & Gamaba 2016). I also noted the amount of time that the demonstrator cricket spent in or adjacent to the water petri dish. The demonstrator cricket was counted as adjacent if it was within a head's length away from the water dish. There were at least ten minutes between each training trial or test trial.

The social learning test trials

During the test trials, the focal cricket was placed back in the maze, but now there were two water dishes, one on each side. A cotton ball soaked in 0.5 ml of strawberry extract was placed behind one dish, and a cotton ball soaked in 0.5 ml of vanilla extract was placed behind the other. One of these odors would have been associated with the demonstrator during the training trials, and the other had not been previously experienced by the focal cricket. The side for each odor was switched on an LRRLRLLR order.

Each test trial lasted until the cricket made a choice and drank from a petri dish, or until ten minutes had passed without the cricket taking a drink. We continued the test trials until the individual either drank during two separate trials or until it ran six total trials.

I tested for social learning using two different criteria: the choice made (i.e. which side and which odor was associated with the water dish that the cricket chose to drink from) the first time a cricket drank during the test trials, and the choice made during the first two times the cricket drank during the test trials. I tested a total of thirty-two crickets and excluded seven individuals because they did not drink during the test trials.

I expected that, if the crickets had socially learned, then they would exhibit a preference to drink on the side containing the odor that had been brushed on the demonstrator cricket and considered this behavior to be the ‘correct’ choice. The disadvantage of looking at just the first choice is that some focal crickets could have chosen the correct side by chance, rather than because they had made the association between the odor and water reward. I therefore examined an additional criterion of whether the first two choices made by the cricket were correct. However, this criterion also has a disadvantage, because with additional trials there was the possibility that the cricket was beginning to make associations between the odor and reward that were unrelated to previous social learning. Note that for both criteria we excluded trials in which the cricket did not make a choice, so our criteria are based on the first/second choice, not necessarily the action on the first/second trial.

Analysis

Repeatability tests were run using the rptR package (Stoffel et al 2017) to check if neophobia or latency to emerge were personality traits (i.e. were significantly repeatable).

Both time to exit shelter and time to come into contact with the object (neophobia) were modeled as gaussian variables, with the object that was being used as the novel object as an explanatory factor, and individual ID as a random factor. Repeatability was also calculated for the time that the crickets spent near each other and the time that the demonstrator cricket was near a water dish during the training trials. For these tests, the ID of the focal cricket was a random factor. A Gaussian repeatability test was also run on the aggression scores of the females across the eight training trials (calculated as in Chapter 1) to determine if aggressive behavior was a personality trait.

A generalized linear model from the binomial family was used to test if the likelihood of social learning (separate models were used for the first choice and first two choices criteria) was related to the following variables: the average amount of time the focal cricket spent with an antenna-length of the demonstrator cricket during the training trials, the average latency to exit the shelter of the focal cricket, the odor associated with the demonstrator, the number of trials in which the focal cricket drank during the training trials, the number of trials in which the demonstrator cricket drank during the training trials, and the random effect of the ID of the focal cricket (Bates et al. 2015). Aggression, the time it took for a cricket to touch a novel object, and the time the demonstrator cricket spent near the water were not included in the models, as none of these variables were significantly repeatable. Seven crickets were removed from the analysis due to not drinking from the water during the test trials.

A two-tailed binomial test was used on the number of times the social learning criteria were met or not with both the first choice and the first two choices criteria to see if the overall pattern of choices deviated from the chance expectation, giving evidence for social learning in the population as a whole. The probability of choosing the correct side for the first choice under the null expectation of random choice was 0.5, and the probability of choosing the correct side for the first two choices was 0.25.

RESULTS

Repeatability results

The time to exit the shelter was significantly repeatable (R= 0.499, SE= 0.091 p> .0001), but the time to come into contact with the novel object (neophobia) was not significantly repeatable (R= 0.169, SE= 0.102, p= 0.078). The amount of time that the focal cricket and the demonstrator cricket spent near each other was significantly repeatable (R= 0.086, SE= 0.056, p= 0.023), but the amount of time that the demonstrator spent near the water was not (R= 0.06, SE= 0.047, p= 0.098). Aggressive behavior was also not repeatable (R= 0.046, SE= 0.044, p= 0.162). As aggression and neophobia were not repeatable, these variables were not included in the social learning models.

Social learning results

Out of twenty-five crickets, only five crickets met the criterion of choosing correctly on the first two choices (Table 11). Eight crickets out of twenty-five met the criterion of choosing correctly on the first choice (Table 11). In neither case was there a significant deviation from chance performance (binomial test; first choice criterion, p=0.108; first two choices criterion, p=0.652). There was no effect of any of the explanatory variables on whether an individual met either the first-choice or first two choices criteria (Tables 12 & 13). Possible side biases during the training trials also appear to have not been a major factor on the choice of which side to drink from during the test trials: of the six crickets that had a left side bias (i.e. crickets that drank more from the left side than from the right side during the training trials), only one individual drank from the left side both times during the test trials. There were ten crickets with a right-side bias in the training trials, but again, only one cricket proceeded to drink from the right side twice during the test trials.

Focal crickets drank more often in the training trials than the demonstrator crickets, with focal crickets drinking in roughly 65.3% of the trials, and the demonstrator crickets drinking in only 27 % of the trials. About 61% of the demonstrator's drinks occurred in the first four training trials, and in 74% of the trials, a demonstrator drank in one of the first three trials.

Discussion

Very few crickets met the social learning criteria for either the first choice (n=8/25) or for the first two choices (n=5/25). The number of crickets that met either social learning criteria was no different from the number of crickets that would have met the criteria through random chance. Thus, there is no evidence that social learning took place in this experiment. Aggressive behavior and latency to exit the shelter were not significant predictors of whether or not individuals met the learning criteria, nor was the odor of the reward or how often the focal cricket drank during the training trials.

There was a trend towards an effect of the number of times the demonstrator cricket drank during the training trials on how likely the focal cricket was to meet the learning criteria, with the results actually trending towards individuals being less likely to meet the criterion if the demonstrator cricket drank more.

Why social learning was not observed

There are several potential explanations for why social learning was not observed. One possibility is that focal crickets were not able to make a connection between the odor and the reward by observing the demonstrator cricket's behavior. It could be that the focal cricket required more than eight training trials to learn to associate the odor with the reward.

In Chapter 1, I showed that many crickets required more than eight trials before they met the criterion for learning to associate an odor with a reward in a simple association task, so it could be that many individuals would require more than eight trials in order to learn to associate the odor with reward in this more complex setup in which the odor was brushed onto the demonstrator cricket.

There is individual variation in social learning in some species (Kurvers et al. 2010, Aplin et al. 2013), so while some individuals could have learned in eight training trials, this could explain why the learning criterion was not met in the majority of the crickets tested. It could also be that there was not always a clear connection between the demonstrator's odor and the reward. This could have happened in cases where the demonstrator drank until it may have been satiated while the focal cricket was in a different arm of the maze, causing the demonstrator cricket to not drink in later trials that day in front of the focal cricket. In around 35% of the trials in which a demonstrator drank, the focal cricket did not drink. There could have also been cases where the demonstrator cricket was not very good at demonstrating due to only having two training trials before the trials with the focal cricket began.

Another possible explanation for why most crickets did not meet the criterion for social learning could be because there was relatively little benefit to obtaining a reward by social learning rather than directly searching for the reward. This can be shown in honey bees, or *Apis mellifera,* where often times various bees would ignore a waggle dance as it did not make sense for the bees to use the public information from other bees when an individual's private information provided resources as well (Grüter et al. 2008, Grüter & Ratnieks 2011). The maze was also small enough that individuals could have learned where water could be found by the end of all the training trials, regardless of whether they followed a demonstrator cricket or not to the water.

There was no aversive stimulus in my experiment to punish the cricket for not learning, so there may have been less need or motivation to socially learn the association between odor and reward. In one demonstration of social learning in wood crickets, *Nemobius sylvestris,* crickets learned anti-predator behaviors from conspecifics, and these behaviors likely have a strong impact on individual survival (Coolen et al. 2005). Another demonstration of social learning in the field cricket *Gryllus bimaculatus* showed that the crickets were capable of socially learning to associate an odor with a source of water, using a similar approach to my experiment except that this previous study there was an also aversive stimulus paired with another odor (Ebina & Mizunami 2020).

Conclusion

Even though this study did not find any connection between meeting the social learning criterion and personality, there is still evidence from other work that personality may play a role in social learning, in vertebrates at least (Trompf & Brown 2014, Kurvers et al. 2010, Carter et al. 2014). The proactive-reactive axis has been shown to influence the degree to which individuals are willing to make use of public information and socially learn (Aplin et al. 2013, Trompf & Brown 2014). However, there are contradictory findings on how the proactive-reactive axis is related to social learning, with reactive individuals using public information more often in some cases (Kurvers et al. 2010, Smit & Oers 2019), whereas in other cases more proactive individuals have been shown to use public information more (Carter et al 2014, Bouchard et al 2007). More research is needed to determine exactly how personality affects social learning, as it could be that proactive and reactive individuals have different social learning strategies, similar to how proactive and reactive individuals sometimes have different asocial learning strategies (Sih & Del Giduce 2012). More research in animal personality should be focused on how personality affects social learning, as personality has been shown to affect social networks, which often also influence how information gets spread throughout a population (Kulahci et al. 2018).

TABLES AND FIGURES

Table 2.1- Performance during the test trials

First two choices criterion		
Both choices correct	One choice correct, one choice incorrect	Both choices incorrect
5	11	9
First choice criterion		
First choice correct	First choice incorrect	
8	17	

The number of crickets making each combination of correct (i.e. drinking from the dish with the odor that was associated with the demonstrator) and incorrect (i.e. drinking from the dish with the odor that was not associated with the demonstrator) choices both for the first choice and first two choices criteria.

Table 2.2- Effects on likelihood of choosing correctly on the first choice in the test trials

Variable	Estimate	Std. Error	Z score	P value
Latency to exit	0.958	0.944	1.015	0.310
Number of focal drinks in training trials	-0.067	0.463	-0.145	0.885
Number of demonstrator drinks in training trials	-1.104	0.565	-1.954	0.051
Average time near demonstrator	-1.839	1.839	-1.000	0.317
Demonstrator odor (vanilla)	-2.481	1.595	-1.556	0.120

Results for a binomial GLMM that tested effects on the first-choice criterion during the test trials. The reference level for the demonstrator odor was the strawberry odor.

Table 2.3- Effects on likelihood of making the first two choices correctly in the test trials

Variable	Estimate	Std. Error	Z score	P value
Latency to exit	4.712	7.038	0.669	0.503
Number of focal drinks in training trials	-0.929	3.475	-0.267	0.789
Number of demonstrator drinks in training trials	-12.788	6.814	-1.877	0.061
Average time near demonstrator	-16.383	17.812	-0.920	0.358
Demonstrator odor (vanilla)	-5.870	9.596	-0.612	0.541

Results for a binomial GLMM that tested effects on meeting the first two choices criterion during the test trials. The reference level for the demonstrator odor was the strawberry odor.

Figure 2.1- The y-maze was used for the social learning trials, with one cricket exploring the maze. On the right arm of the maze is a petri dish with water, and above it is a petri dish with a cotton ball, which was the configuration used for the training trials. During the test trials, there were two petri dishes on both arms, and the cotton ball on each side was soaked in a different extract.

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