Social and Individual Learning in the Fall Field Cricket

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Abstract

Social learning is a well-studied process in vertebrates, yet insect social learning studies have historically neglected solitary insects. To bridge this gap, I investigated whether the fall field cricket, *Gryllus pennsylvanicus*, could use individual and social learning to associate water with visual and odour cues. Demonstrator crickets had firsthand experience sampling water paired with cues, and observer crickets watched the demonstrators. I therefore tested demonstrators for individual learning and observers for social learning. I tested for learning by measuring cue preference in the absence of water. When quantifying cue preference by the proportion of time spent near rewarded cues, there was no evidence of individual or social learning. However, when quantifying cue preference by the first cue investigation (>3 seconds) during the test, crickets showed evidence of individual but not social learning. There was also a small effect of cue type on learning. These results differ from previous studies that found social learning in other species of crickets. The findings highlight that there are interspecific differences in learning and social behaviour, and that the method of quantifying learning can influence the outcome.

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researcher looked like, and you fueled my love for cognition. I can only hope that you would be proud of what I’ve accomplished.

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Introduction

Learning is a crucial process that helps animals in navigating life's demands (Morand-Ferron, 2017). It can be defined broadly as a change in state due to experience (Shettleworth, 2009). A range of animals across taxa, irrespective of size or perceived complexity, use learning to gain information about their environment and adjust their behaviours accordingly (Dukas, 2009; Shettleworth, 2009).

Learning is important to survival and reproduction. For example, Dukas (2000) found that grasshoppers (*Schistocerca americana*) who learned to seek a balanced diet had higher growth rates than grasshoppers who did not learn. Raine and Chittka (2008) showed that bumblebee colonies (*Bombus terrestris*) that were comprised of better learners had higher foraging success, which is a reliable proxy measure of fitness. Similar fitness impacts are also seen in wild individuals. Male New Zealand robins (*Petroica longipes*) with more accurate spatial memory produced more offspring, produced more independent offspring, and brought larger prey to the nest (Shaw et al., 2019). Similarly, female Australian magpies (*Cracticus tibicen dorsalis)* with greater general cognitive ability had higher reproductive success, by multiple measures (Ashton et al., 2018). In great tits (*Parus major*) high problem-solving ability was found to be linked with both benefits and costs: good problem-solvers had larger clutch sizes, but were more likely to abandon their nests when disturbed (Cole et al., 2012). These are only a few studies that demonstrate the overall impact that cognition can have on fitness (reviewed in Morand-Ferron et al., 2016; Morand-Ferron 2017; Boogert et al., 2018; Pravosudov, 2022).

Along with individual learning, a variety of animals also learn by watching others. Social learning is a process that involves acquiring others' behaviours through observation. Individuals can use social learning to gain environmental information (e.g., about mate choice, foraging, and anti-predator behaviour) without firsthand experience (Reviewed in Galef & Laland, 2005). As a result, gaining information via social learning can be less costly than gaining information via individual learning, which often involves much trial and error (Galef & Laland, 2005). Social learning is an important mechanism that contributes to the spread of ideas and culture (Boyd & Richerson, 1985).

Historically, much of the social learning literature has focused on vertebrates like rats, fish, and birds (Galef & Laland, 2005). Social learning and social information use have been observed in insects, though most studies on insects have focused on eusocial Hymenoptera (reviewed in Leadbeater & Chittka, 2007; Grüter & Leadbeater, 2014). Like social learning, social information use involves monitoring others' interactions with the environment (Danchin et al., 2004). However, I distinguish the two here, in that social learning is tested without a demonstrator present, and social information use is tested with the social cues still readily available (e.g., Webster and Laland, 2017). Despite being well-studied in eusocial insects, it is critical to test social learning in solitary insects as well, as the frequency of social learning could be impacted by the high relatedness of social insect societies (Grüter & Leadbeater, 2014). Findings are mixed when it comes to non-eusocial insects – there is no evidence of social learning in migratory locusts (*Locusta migratoria*) (Dukas & Simpson, 2009) or in desert locusts (*Schistocerca gregaria*) (Lancet & Dukas, 2012). In fruit flies (*Drosophila melanogaster*), there is evidence of social information use (Mery et al., 2009; Foucaud et al., 2013), and several experiments have shown social learning. For example, females are more likely to lay eggs on a novel food when they have observed another female with eggs on that food (Sarin & Dukas, 2009). Female fruit flies also use mate choice copying, in which they use social learning to choose which males to mate with (Dagaeff et al., 2016; Danchin et al., 2018; Nobel et al., 2018). However, there is no evidence of mate choice copying in *D. serrata* (Auld et al., 2009).

To my knowledge, there have only been two studies to date that have focused on social learning in crickets. Coolen et al. (2005) found that young wood crickets (*Nemobius Sylvestris*) learned to avoid predators by watching experienced individuals. Crickets were given a period of six hours with a demonstrator who had just spent days with a predator. After spending time with an experienced demonstrator, naïve crickets made themselves less visible to predators. Similarly, Ebina and Mizunami (2020) found that *Gryllus bimaculatus* crickets use social learning. Adult male crickets learned to avoid an odour that was paired with a dead conspecific, which acted as a demonstrator. Crickets also learned to prefer an odour that was paired with water by watching a demonstrator drink water paired with that odour.

My study builds on Ebina and Mizunami's (2020) study by using similar methods to investigate social learning in the fall field cricket (*Gryllus pennsylvanicus*). *G. pennsylvanicus* is a solitary insect species native to North America. Their social interactions in the wild are generally limited to territorial interactions and mating events. Females lay their eggs during the fall and leave them to undergo an obligate diapause period over the winter (Weissman & Gray, 2019, p. 50), resulting in no opportunity for parents to interact with their offspring.

While there are no published studies on learning in *G. pennsylvanicus*, several studies have shown that other field crickets (crickets in the genus *Gryllus*) can learn. Most of these studies have investigated individual learning in *G. bimaculatus*. For example, associative learning studies reveal that *G. bimaculatus* can be trained to prefer certain odours and colours (reviewed in Mizunami et al., 2013; Ebina & Mizunami, 2020). These crickets can also learn in a water maze-like paradigm, in which they must find a cool spot in an arena with a heated floor

(Weissnitzer et al., 2008). Texas field crickets (*G. texensis*) can learn food locations in a radial arm maze, likely using visual cues (Doria et al., 2019; Kozlovsky et al., 2022).

Using a classical conditioning procedure, I investigated whether the fall field cricket could learn individually and socially by associating water with visual and/or olfactory cues. By testing for individual and social learning within the same experiment, I was able to control for whether crickets were A) able to learn individually but not socially, or B) incapable of learning individually *or* socially under these conditions. I hypothesized that *G. pennsylvanicus* would be able to learn individually, given the various studies showing associative learning capabilities in *G. bimaculatus* (Mizunami et al., 2013). I also hypothesized that, like *N. Sylvestris* and *G. bimaculatus*, *G. pennsylvanicus* crickets would use social learning.

Methods

Cricket Care

Wild-caught crickets were collected yearly in the late summer to early fall. Crickets were caught in the Ottawa–Gatineau area and added to the colony yearly, which helped to prevent inbreeding and maintain the colony's genetic integrity. Crickets were housed in opaque group containers (52 x 39 x 42 cm) under a 12:12 light/dark cycle at 25°C. Containers were maintained three times per week and crickets were provided with cardboard shelter, along with powdered rodent diet (Envigo Teklad Rodent Diet 8604) and water ad libitum.

I isolated male and female juvenile crickets just before their final moult and housed them in clear individual plastic containers (11cm diameter x 8cm tall) with food, water, and cardboard shelter. Each cricket was assigned a unique identifier and participated in the experiment once they reached adulthood. Individuals in the experiment were used 2 to 16 days after their final moult, during their prime adulthood (Dixon and Cade, 1986).

Overview

To test learning, I used a classical conditioning procedure consisting of a training phase and a test phase, adapted from Ebina and Mizunami's (2020) social learning study. For the training phase, an observer watched a demonstrator choose between two drinking sources: one containing water paired with one set of cues, and one containing saltwater paired with the opposite set of cues (Fig.1). In the test phase, an individual cricket chose between the two cue sets (Fig. 2). The demonstrator was tested for individual learning, as they had firsthand sampling experience; the observer was tested for social learning, as they only had experience watching the demonstrator. Observers were tested without a demonstrator present to test for social learning, rather than social information use (Webster & Laland, 2017). Groups of crickets learned if, on average, they preferred the cues that were paired with water in the training phase.

Groups

Crickets were randomly divided into demonstrators and observers. Demonstrators and observers were then each sub-divided into two more groups: group A and group B. Group A had water (appetitive) paired with cue set A and saltwater (aversive) paired with cue set B. Group B had water paired with cue set B and saltwater paired with cue set A. Thus, Group A was conditioned to prefer cue set A and group B was conditioned to prefer cue set B. Cue set A was comprised of apple extract (OliveNation Pure Apple Extract), diluted in a 3:1 water to extract ratio, a green drinking container, and three green square shapes placed on and around the drinking container. Cue set B was comprised of diluted banana extract (OliveNation Pure Banana Extract), a blue drinking container, and three blue triangle shapes placed on and around the drinking container.

Training phase

24 hours before training, crickets were weighed then deprived of water to maximize their motivation to seek water (Rowe & Healy, 2014). 40 minutes before training, crickets were weighed again to quantify their extent of water loss. Training took place in a clear acrylic container (20 x 15 x 11 cm) with a net dividing the space between the demonstrator and the observer (Fig. 1). The observer's side floor was raised 1.5 cm to allow for easy observation. The floor was covered in fresh paper towel before each trial to allow for easy movement and to reduce odour cues from previous crickets. On the demonstrator's side of the container, there were two drinking containers made of an upside-down plastic cup 4.5 cm in diameter and 1.5 cm tall. A ball of gauze soaked in either water or saltwater was placed in a large hole on top of the drinking container. Odours diffused from filter papers underneath the cup, which were soaked in apple or banana extract, diluted in a 3:1 ratio. Small holes in the top and sides of the cup allowed for odour diffusion. Drinking containers were replaced between trials. Both observers and demonstrators were allowed a four-minute acclimation period in a 4.5 cm diameter, 5 cm tall plastic container in the arena, placed in the middle of their respective sections. Acclimation was followed by a 10-minute training period in which the demonstrator was allowed to sample from either drinking container, and the observer was allowed to watch. Preliminary experiments revealed that demonstrator crickets have a strong aversion to saltwater, reliably cueing water without prior experience.

Following the training period, both crickets were given a rest period of four hours, during which they were placed back in their home containers without water. This rest period aimed to test long-term memory, as social learning is characterized by a long-term change in behaviour (Mesoudi et al., 2016). This period also gave demonstrator crickets time to become thirsty again.

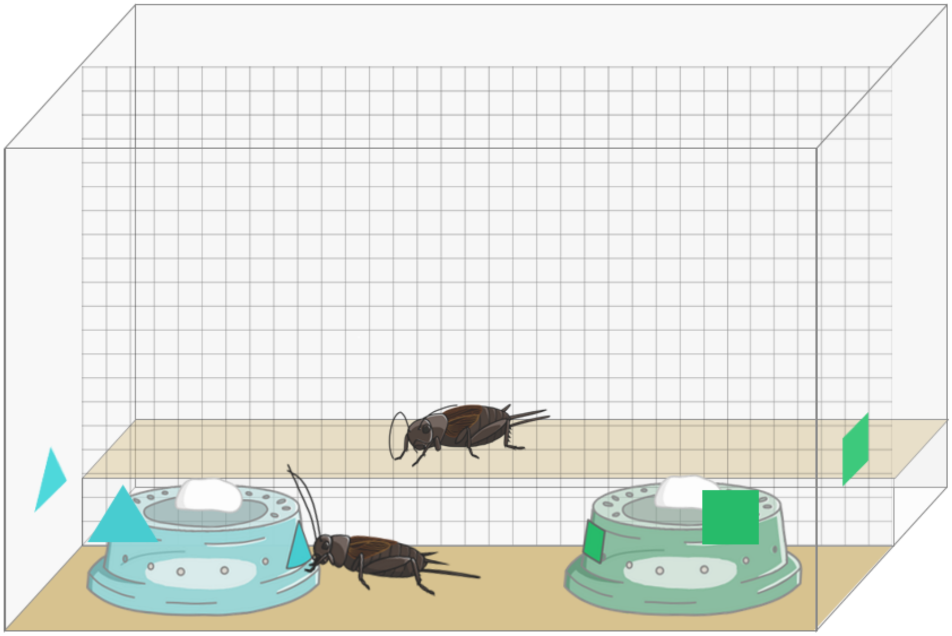

Figure 1. Training arena. A demonstrator can sample from two drinking sources paired with different cues, while the observer is free to watch from behind a net. Odours diffuse from under the drinking containers while coloured shapes lie on and around the containers.

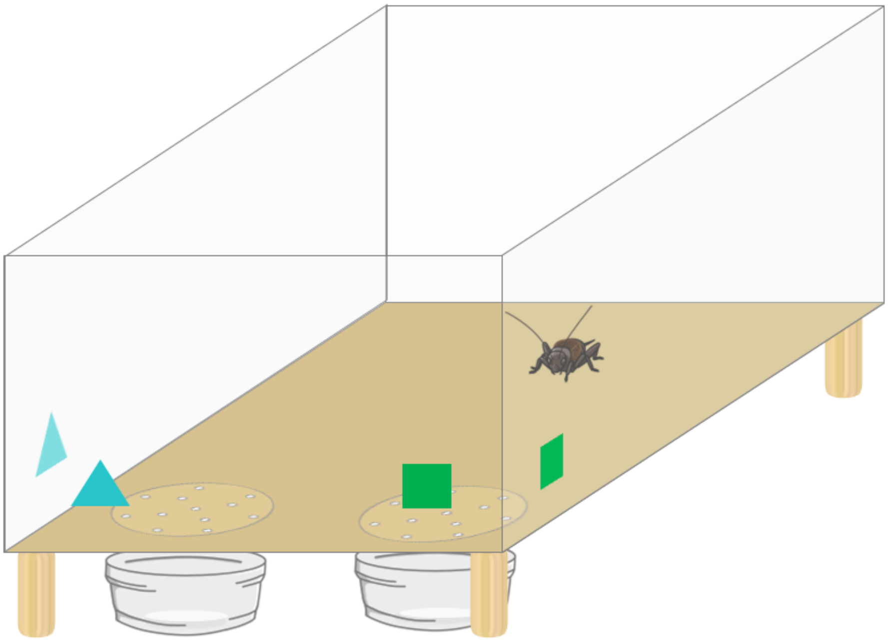

Figure 2. Test arena. A demonstrator or observer cricket can freely roam a container with two cue zones. Cue zone A (pictured right) had apple odour diffusing from underneath the floor and green squares placed nearby. Cue zone B (pictured left) had banana odour diffusing from underneath the floor and blue triangles placed nearby.

Test phase

Testing determined the crickets' cue preference in the absence of water and saltwater. Tests took place in a clear plastic container (34 x 21 x 12 cm; Fig. 2). The container was mounted 5 cm off the ground using wooden dowels. Paper towel covered the ground for easy movement and for easy removal of any scents between trials. The testing area had two circular cue zones each 4.5 cm in diameter and 4.5 cm apart, with holes in the floor to allow for odour diffusion from underneath. Cue zones had filter papers soaked in diluted extract placed underneath the container floor. Cue zone A had apple odour beneath the floor and green squares placed on the walls nearby the cue zone. Cue zone B had banana odour beneath the floor and blue triangles placed on the walls nearby. Cue zone locations (left/right) were randomized, and locations were swapped halfway through the test to ensure the cricket is displaying a cue preference, rather than a side preference.

Each cricket was given a four-minute acclimation period, followed by a four-minute test period. During the test, the cricket was free to roam the container and explore the cue zones. All trials were recorded using a Canon Vixia HF R400 video camera, and later analyzed using BORIS (Friard & Gamba, 2016). Video scorers were blind to group assignment and recorded the events where a cricket's head or antennae were within each cue zone. As a result, the total amount of time in the rewarded zone and the unrewarded zone were quantified. The first cue zone visits >3 seconds were also noted.

Following the test, crickets were euthanized and photographed using a Zeiss Stemi 305 Stereo Microscope with an Axiocam 208 camera. Using ImageJ (Rasband, 2018), head width (maximal distance from eye to eye), pronotum width (maximal transverse distance across the pronotum), and pronotum length (maximal sagittal distance down the pronotum) were recorded from each photograph.

Statistical Analysis

Statistical analyses were performed using R version 4.2.2 (R Core Team, 2022), except for PCA, which was performed in JMP PRO 16.2. Crickets who explored the cue zones for less than a total of 5 seconds were omitted from analysis, as they were deemed to be unmotivated.

Through principal component analysis, measurements of head width, pronotum width, and pronotum length, as well as weight prior to water deprivation, were used to make an overall measure of body size. PC1 size by sex explained 88.9% of the variation in female size (eigenvalue = 3.56; eigenvector loadings: 0.49-0.51 for the four size variables) and 91.1% of the variation in male size (eigenvalue = 3.64; eigenvector loadings: 0.50-0.51 for the four size variables).

To see whether demonstrators and observers preferred the rewarded zone, I calculated the proportion of time spent in the rewarded zone versus the unrewarded zone, and I did two one-sided t-tests. The first tested if the demonstrators had a mean proportion of time spent in the rewarded zone that was greater than 0.5. I repeated this test for observers.

I created a beta-binomial generalized linear mixed model (GLMM) to assess cue zone preference, using the package aod (Lesnoff & Lancelot, 2012). Cue zone preference was quantified as a proportion of time spent in the rewarded versus the unrewarded cue zone. I included type (demonstrator or observer) and group (A or B) in each model. The full model also included sex, body size, and percent weight lost. Percent weight lost after 24 hours of water deprivation was included to quantify motivation to seek water. An interaction between body size and sex was also included. I added an observation-level random effect to moderate for overdispersion.

I used Aikake's Information Criterion adjusted for small sample size (AICc) for model selection, using the package MuMIn (Bartoń, 2022). I determined the top models with ΔAICc values <4 and performed model averaging of this candidate model set.

After the initial analysis, it occurred that crickets may be showing learning through other means. Thus, I performed a second analysis examining the first cue zone visit that lasted for longer than three seconds. I chose to use the first visit longer than three seconds, rather than the first zone visit overall, because this 3-second threshold targets crickets that are investigating the zone rather than passing through by chance. To see if the crickets were more likely than chance to investigate the rewarded zone than the unrewarded zone, I performed a one-sided exact binomial test on crickets in each group (A or B) and type (demonstrator or observer).

I created a second model using the first zone visit >3 seconds as the dependent variable. Using a binary generalized linear model, I underwent the same model selection process with the same predictors as before: group, type, body size, % weight lost, and a sex*body size interaction term.

Results

A total of 154 crickets were tested, with 107 crickets exploring cue zones for more than 5 seconds. Of the 107 crickets, the total time exploring cue zones ranged between 5 and 68 seconds (Fig. 3). Two crickets who met the 5 second criteria were missing body size data and were omitted from analysis.

If individuals learned to associate cues with the reward, we would expect that the demonstrators would spend >50% of their time with the rewarded zone, compared to the unrewarded zone. Instead, the mean proportion of time spent in the rewarded zone was not significantly greater than 0.5 for demonstrators (mean=0.515, sd=0.213; one-sided t-test, n=53, p=0.307), suggesting that individuals in general did not learn. Observers also did not differ significantly from 50%, suggesting that individuals in general did not exhibit social learning (mean=0.515, sd=0.213; one-sided t-test, n=53, p=0.827) (Fig. 4).

The first model characterized cue preference by the proportion of time spent in the rewarded versus the unrewarded zone. There were 6 models within 4 ΔAICc of the top model (Table 1). None of the top models included the body size by sex interaction. In the averaged model, type (demonstrator or observer) was not a significant predictor of time spent in cue zones.

Group (A or B) was also not a significant predictor of time spent in cue zones. Thus, neither of the manipulated variables had an effect on cue preference. None of the other variables tested (body size, percent weight lost, sex) were significant predictors of cue preference (Table 2).

76 crickets had a visit to a cue zone that lasted longer than three seconds. Demonstrators were 65% likely to have a first visit >3 seconds to the rewarded zone (Fig. 5A). As a result, they were marginally significantly more likely to visit the rewarded zone than the unrewarded zone (exact one-sided binomial test, n=37, p=0.049). Therefore, demonstrators may have learned to associate the reward zones with the cues. Conversely, observers were only 49% likely to have a first visit >3 seconds to the rewarded zone. They were not significantly more likely to visit the rewarded zone than the unrewarded zone (n=39, p=0.625), indicating no evidence of social learning.

There was also a slight effect of cue type on the probability that the cricket investigated the rewarded zone first, as group A individuals were 64.1% likely to visit the rewarded zone first, and group B individuals were 48.6% likely to visit the rewarded zone first. However, this difference did not quite reach statistical significance (exact one-sided binomial test, Group A: n=39, p=0.054; Group B: n=37, p=0.629).

The second model characterized cue preference by the first cue zone visit >3 seconds. There were 6 models within 4 ΔAICc of the top model (Table 3). None of the top models included the interaction between sex and body size. Both group (A or B) and type (demonstrator or observer) were not significant predictors of the first cue zone investigation, despite the previously discussed differences. In addition, sex, percent weight lost, and body size were not significant predictors of first visits (Table 4).

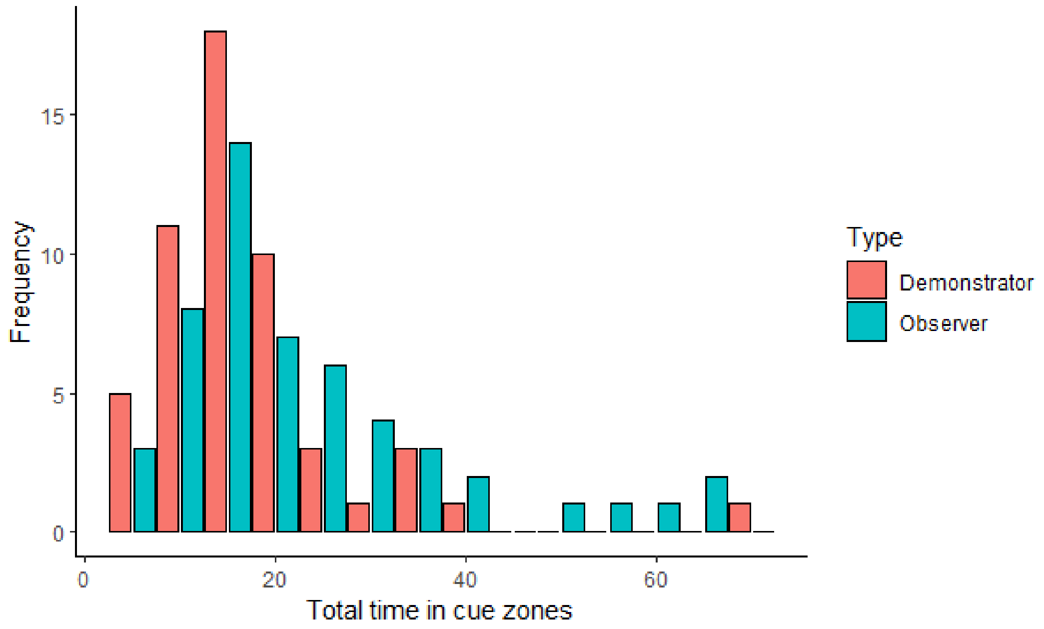

Figure 3. Total time spent in cue zones (seconds) by demonstrators (mean=17.3s) and observers (mean=22.9s).

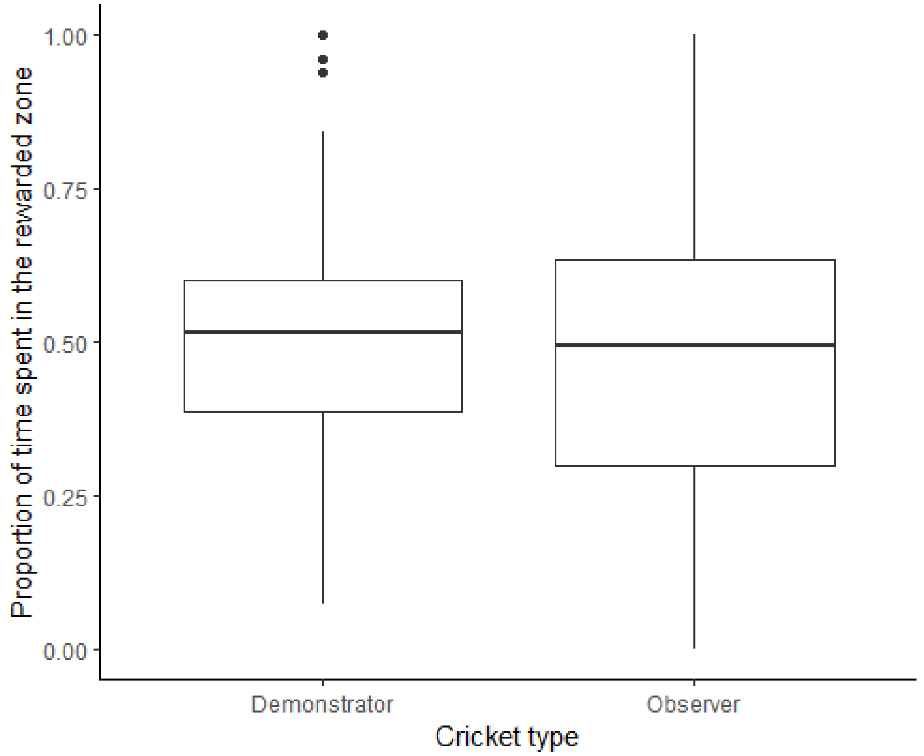

Figure 4. Proportion of time spent in the rewarded zone by demonstrators and observers.

Model	df	AICc	Delta	Weight
Group+Type+(1|O)	4	1068.98	0	0.35
Group+Type+Sex+(1|O)	5	1069.76	0.78	0.23
Group+Type+Body Size+(1|O)	5	1070.83	1.85	0.14
Group+Type+Weight Lost+(1|O)	5	1071.18	2.20	0.12
Group+Type+Sex+Body Size+(1|O)	6	1071.65	2.68	0.09
Group+Type+Weight Lost+Sex+(1|O)	6	1071.97	3.00	0.08

Table 1. Models within <4 ΔAICc of the top model, their degrees of freedom, AICc, delta values, and weights. Full model: Time rewarded/unrewarded ~ Group + Type + Sex + Body Size + % Weight Lost + Sex*Body Size + (1|O)

Predictors	Estimate	Standard Error	*P*
Intercept	0.257	0.180	0.152
Group (B)	-0.154	0.181	0.393
Type (Observer)	-0.259	0.181	0.153
Sex (Male)	-0.087	0.157	0.578
Body size	0.007	0.026	0.801
% Weight Lost	0.0001	0.009	0.990

Table 2. Full average results from models <4 ΔAICc of the top model. Full model: Time rewarded/unrewarded ~ Group + Type + Sex + Body Size + % Weight Lost + Sex*Body Size + (1|O)

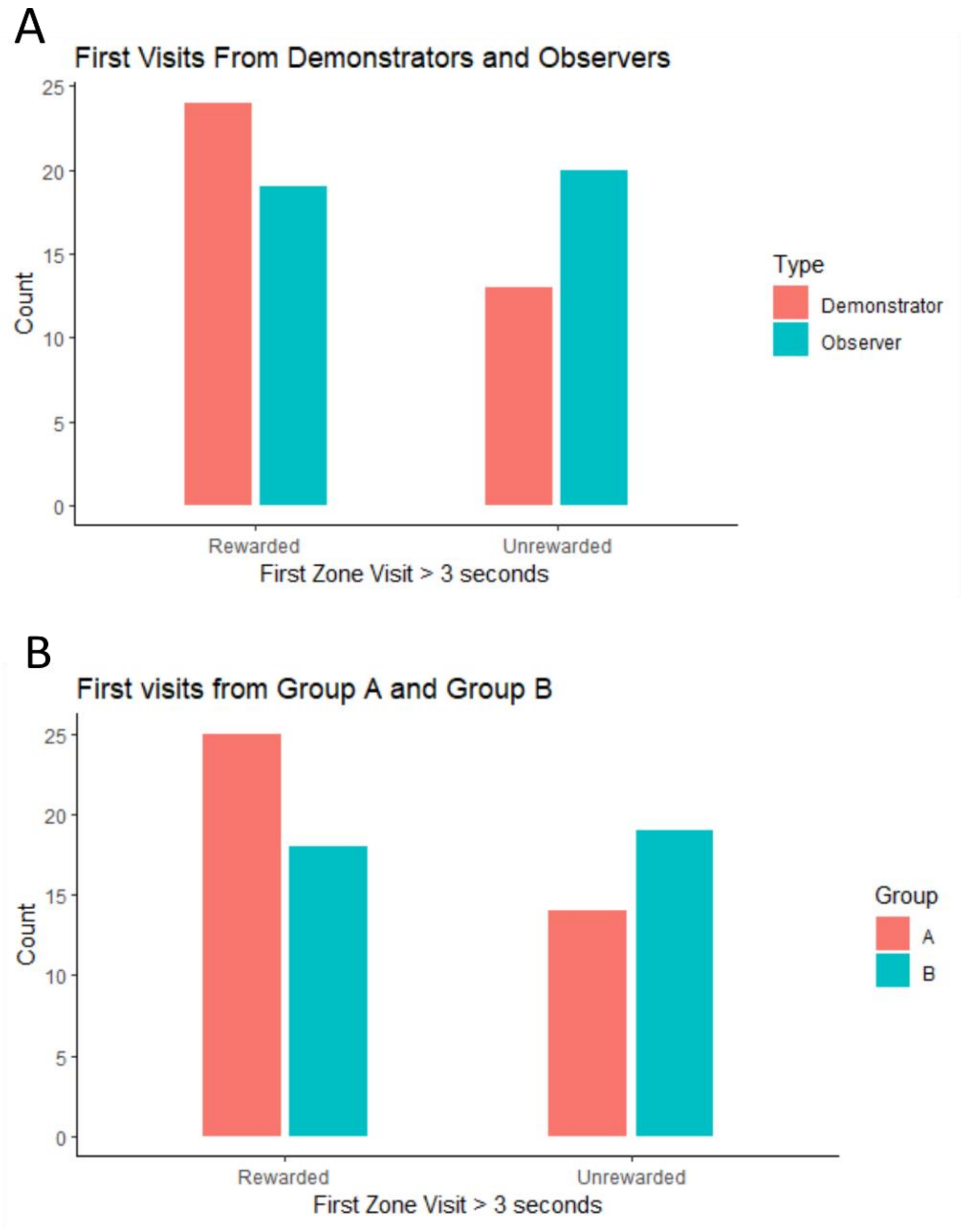

Figure 5. A) First visit to a cue zone >3 seconds from demonstrators and observers, and B) First visit to a cue zone >3 seconds from group A and group B.

Model	**df**	**AICc**	**Delta**	**Weight**
Group+Type	3	106.22	0	0.39
Group+Type+Sex	4	107.59	1.37	0.19
Group+Type+Weight Lost	4	108.29	2.07	0.14
Group+Type+Body Size	4	108.44	2.22	0.13
Group+Type+Weight Lost+Sex	5	109.12	2.90	0.09
Group+Type+Body Size+Sex	5	109.88	3.67	0.06

Table 3. Models within <4 ΔAICc of the top model, their degrees of freedom, AICc, delta values, and weights. Full model: First visit ~ Group + Type + Sex + Body Size + % Weight Lost + Sex*Body Size

Predictors	**Estimate**	**Standard Error**	***P***
Intercept	0.953	0.565	0.097
Group (B)	-0.662	0.485	0.179
Type (Observer)	-0.714	0.485	0.147
Sex (Male)	-0.177	0.390	0.653
% Weight Lost	0.014	0.057	0.808
Body size	0.001	0.058	0.983

Table 4. Full average results from models <4 ΔAICc of the top model. Full model: First visit ~ Group + Type + Sex + Body Size + % Weight Lost + Sex*Body Size

Discussion

This study provides initial evidence for individual learning in the fall field cricket, *Gryllus pennsylvanicus*. During testing, demonstrator crickets were more likely to first investigate the rewarded cue zone than expected by chance. However, this preference is not reflected in the overall proportion of time spent in the rewarded versus unrewarded zones, as they did not spend more than half of their time in the rewarded zone. It is possible that once demonstrator crickets found that there was no water present, they explored the arena more fully. Overall, these findings suggest that the first zone investigated may be more important than the proportion of time spent in cue zones for measuring learning under these conditions.

Conversely, there is no evidence that fall field crickets exhibit social learning. During testing, observers were no more likely to first investigate the rewarded zone than the unrewarded zone. They were also no more likely to spend more time in the rewarded zone than in the unrewarded zone. These differences between demonstrators and observers likely result from the demonstrators having firsthand experience sampling water paired with the visual and odour cues, whereas observers could only watch this. Crickets may either favour personal information over social information, or they might not have evolved the ability to learn socially. Dukas (2010) outlined that certain life history traits, like lack of parental care and lack of overlapping generations, may limit social learning. *G. pennsylvanicus* does not exhibit parental care, and generations do not overlap, which could contribute to a lack of social learning.

My findings differ from those obtained in Ebina and Mizunami's 2020 social learning study in *G. bimaculatus*. Despite extending the training period, reducing the time between training and testing, and providing visual cues in addition to olfactory cues, *G. pennsylvanicus* only in part showed individual learning and did not show social learning within the allotted time. The observed differences likely reflect interspecific differences in learning ability – a procedure which was developed for *G. bimaculatus* is simply not suitable to test social and individual learning in *G. pennsylvanicus*. In the future, it would be beneficial to use an established learning task that is more applicable to a variety of solitary insects. The results therefore highlight the importance of not generalizing about the learning abilities of insects after a finding in only one species.

There was a non-significant trend for crickets in group A, who were trained to prefer apple odour and green cues. These crickets were more likely to investigate the rewarded zone than the unrewarded zone first. Crickets in group B, however, were no more likely to investigate the rewarded zone than the unrewarded zone first. A possible explanation for this is that an animal's speed with which they learn an association could depend on their experiences during development, their environment, and natural selection (Rowe & Healy, 2014). Furthermore, animals that encounter certain colours more often in their environment (for example, in their diet) more often might be biased to associate the regularly encountered colour with a reward (Rowe & Healy, 2014). Crickets could have something in their environment, whether in their recent or evolutionary past, that biases them against or towards learning certain colour associations. Further investigation is needed to ascertain if there are true differences in how cue type impacts learning, and if there are, what the functional causes are.

None of the analyses revealed any evidence of body size or sex having an impact on learning, whether it was characterized by proportion of time in the rewarded zone or by first cue zone investigation. Using weight lost as a metric for motivation, motivation to seek water also had no impact on cue preference. We might have expected these three variables to be associated with learning; cognitive ability sometimes differs by sex (Thornton & Lukas, 2012), though not consistently across species and cognitive tasks. Poor body condition and poor diet (i.e., malnutrition, food restrictions, etc.) can negatively impact the development and maintenance of cognitive skills (reviewed in Buchanan et al., 2013). Further, a thirstier animal might be expected to learn faster, as water is considered more rewarding (Rowe & Healy, 2014). However, I found no evidence of any of these variables impacting cue preference under these conditions.

Some of the individual learning findings are weak statistically and a strongly designed follow-up experiment would be able to test cricket learning better and find clear evidence of an absence or presence of learning. It is possible that the field crickets needed more time to form an association between water and the provided cues. Prolonged or repeated training sessions are common across cricket learning experiments. For example, male *G. bimaculatus* crickets needed at least 8 conditioning trials to form an association between water and colour cues (Nakatani et al., 2009). Wood crickets (*N. sylvestris*) learned predator avoidance techniques from a demonstrator after one six-hour training period (Coolen et al., 2005). *Pteronemobius sp.* crickets learned to prefer a side in a y-maze task after 10 rewarded trials (Jaffe & Blanco, 1994). Female Texas field crickets (*Gryllus texensis*) showed spatial learning in a radial arm maze after 4 consecutive days of training (Doria et al., 2019). Taken together, these experiments reveal that a follow-up experiment with repeated training would likely be more robust and effective in studying learning.

There was a large range of cue zone preferences during the test period. Individual variation on cognitive tasks has been shown to be consistent across time (Cauchoix et al., 2018). Future studies could focus on if this variation is repeatable and investigate how and why individuals differ when it comes to learning task performance. For example, some crickets may be better learners, or they may differ in their reliance on social versus private information.

In summary, *G. pennsylvanicus* crickets showed some evidence of individual learning and showed no evidence of social learning. The chosen learning metric influenced these findings. My study makes progress towards understanding the potential for using crickets as a study system for learning. It builds on previous learning studies and highlights the vast differences in learning and social behaviour within a single genus.

References

Ashton, B.J., Ridley, A.R., Edwards, E.K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature, 554,* 364–367. https://doi.org/10.1038/nature25503.

Auld, H., Punzalan, D., Godin, J.J., & Rundle, H. (2009). Do female fruit flies (*Drosophila serrata*) copy the mate choice of others? *Behavioural Processes, 82*, 78–80. https://doi.org/ 10.1016/j.beproc.2009.03.004.

Bartoń K (2022). _MuMIn: Multi-Model Inference_. R package version 1.47.1, https://CRAN.R-project.org/package=MuMIn.

Boogert, N.J., Madden, J. Morand-Ferron, J., & Thornton, A. (2018). Measuring and understanding individual differences in cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences, 373*, 20170280. https://doi.org/ 10.1098/rstb.2017.0280.

Boyd, R. & Richerson, P.J. (1985). *Culture and the evolutionary process*. University of Chicago Press.

Buchanan, K., Grindstaff, J., & Pravosudov, V. (2013). Condition-dependence, developmental plasticity, and cognition: implications for ecology and evolution. *Trends in ecology and evolution, 28*(5), 290–296. https://doi.org/10.1016/j.tree.2013.02.004.

Cauchoix, M., Chow, P.K.Y., van Horik, J.O., Atance, C.M., Barbeau, E.J., Barragan-Jason, G., Bize, P., Boussard, A., Buechel, S.D., Cabirol, A., Cauchard, L., Claidière, N., Dalesman, S., Devaud, J. M., Didic, M., Doligez, B., Fagot, J., Fichtel, C., Henke-Von Der Malsburg, J., … & Morand-Ferron, J. (2018). The repeatability of cognitive performance:

A meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences, 373.* http://dx.doi.org/10.1016/j.nlm.2009.05.003.

Cole, E., Morand-Ferron, J., Hinks, A., & Quinn, J. (2012). Cognitive ability influences reproductive life history variation in the wild. *Current Biology, 22,* 1808–1812. http://dx.doi.org/10.1016/j.cub.2012.07.051.

Coolen, I., Dangles, O., & Casas, J. (2005). Social learning in noncolonial insects? *Current Biology, 15*, 1931–1935. https://doi.org/10.1016/j.cub.2005.09.015.

Danchin, E., Giraldeau, L., Valone, T.J., & Wagner, R.H. (2004). Public information: From nosy neighbors to cultural evolution. *Science, 305*(5683), 487–491. https://doi.org/ 10.1126/science.1098254.

Danchin, E., Nöbel, S., Pocheville, A., Dagaeff, A., Demay, L., Alphand, M., Ranty-Roby, S., van Renssen, L., Monier, M., Gazagne, E., Allain, M., & Isabel, G. (2018). Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. Science, 362(6418), 1025–1030. https://doi.org/ 10.1126/science.aat1590.

Dagaeff, A., Pocheville, A., Nöbel, S., Loyau, A., Danchin, E., & Isabel, G. (2016). Drosophila mate copying correlates with atmospheric pressure in a speed learning situation. Animal behaviour, 121, 163–174. https://doi.org/10.1016/j.anbehav.2016.08.022.

Dixon K.A, Cade W.H. 1986. Some factors influencing male-male aggression in the field cricket Gryllus integer (time of day, age, weight and sexual maturity). *Animal Behavior*, *34*, 340–346. https://doi.org/10.1016/S0003-3472(86)80102-6.

Doria, M., Morand-Ferron, J., & Bertram, S.M. (2019). Spatial cognitive performance is linked to thigmotaxis in field crickets. *Animal Behaviour, 150,* 15–25. https://doi.org/ 10.1016/j.anbehav.2019.01.022.

Dukas, R. (2000). Learning improves growth rate in grasshoppers. *PNAS, 97*(6). 2367–2640. https://doi.org/ 10.1073/pnas.050461497.

Dukas, R. (2010) Social learning in insects. In: Encyclopedia of Animal Behavior (Breed, M. & Moore, J., eds). Academic Press, Oxford, pp. 176–179.

Dukas, R. (2009). Learning: Mechanisms, ecology, and evolution. In Dukas, R. & Ratcliffe, J.M. (Eds.), *Cognitive ecology II* (pp. 7–26). University of Chicago press.

Dukas, R., & Simpson, S. (2009). Locusts show rapid individual learning but no social learning about food. *Animal Behaviour, 78*, 307-311. http://dx.doi.org/10.1016/j.anbehav.2009.05.004.

Ebina, H., & Mizunami, M. (2020). Appetitive and aversive social learning with living and dead conspecifics in crickets. *Scientific Reports, 10*. 1https://doi.org/0.1038/s41598-020-66399-7.

Foucaud, J., Philippe, A., Moreno, C., & Mery, F. (2013). A genetic polymorphism affecting reliance on personal versus public information in a spatial learning task in Drosophila melanogaster. *Proceedings of the Royal Society B: Biological Sciences, 280*. https://doi.org/10.1098/rspb.2013.0588.

Friard, O. & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution, 7*, 1325–1330. https://doi.org/10.1111/2041-210X.12584.

Galef, B.G. & Laland, K.N. (2005). Social learning in animals: Empirical studies and theoretical models. *BioScience, 55*(6), 489–499. https://doi.org/10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2.

Grüter, C. & Leadbeater, E. (2014). Insights from insects about adaptive social information use. *Trends in Ecology and Evolution, 29*(3), 177–184. https://doi.org/10.1016/j.tree.2014.01.004.

Hartig, F. (2022). _DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models_. R package version 0.4.6, https://CRAN.R-project.org/package=DHARMa.

Jaffe, K. & Blanco, M. (1994). Involvement of amino acids, opioids, nitric oxide, and NMDA receptors in learning and memory consolidation in crickets. *Pharmacology, Biochemistry, and Behavior, 47*(3), 493–496. https://doi.org/10.1016/0091-3057(94)90149-X.

JMP®, Version 16.2. SAS Institute Inc., Cary, NC, 1989–2023.

Kozlovsky, D.Y., Porier, M., Hermer, E. Bertram, S.M., & Morand-Ferron, J. (2022). Texas field crickets (Gryllus texensis) use visual cues to place learn but perform poorly when intra- and extra-maze cues conflict. *Learning and Behavior, 50,* 306–316. https://doi.org/10.3758/s13420-022-00532-6.

Lancet, Y., & Dukas, R. (2012). Socially influenced behaviour and learning in locusts. *Ethology 118*, 302–310. https://doi.org/10.1111/j.1439-0310.2011.02014.x.

Leadbeater, E., & Chittka, L. (2007). Social learning in insects – From miniature brains to consensus building. *Current Biology, 17*, 703–713. https://doi.org/10.1016/j.cub.2007.06.012.

Lesnoff, M., & Lancelot, R. (2012). aod: Analysis of Overdispersed Data. R package version 1.3.2, https://cran.r-project.org/package=aod.

Mery, F., Varela, S.A.M., Danchin, E., Blanchet, S., Parejo, D., Coolen, I., & Wagner, R. H. (2009). Public versus personal information for mate copying in an invertebrate. *Current Biology 19*, 730–734. https://doi.org/ 10.1016/j.cub.2009.02.064.

Mesoudi, A., Chang, L., Dall, S.R.X., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology and Evolution*, *31*(3), 215–225. http://dx.doi.org/10.1016/j.tree.2015.12.012.

Mizunami, M., Matsumoto, Y., Watanabe, H., & Nishino, H. (2013). Olfactory and visual learning in cockroaches and crickets. In: Handbook of behavioral neuroscience (vol. 22). (Menzel R., & Benjamin, P. R., eds.). Elsevier.

Morand-Ferron, J., Cole, E., & Quinn, J. (2016). Studying the evolutionary ecology of cognition in the wild: A review of practical and conceptual challenges. *Biological reviews, 91*(2), 367–389. https://doi.org/ 10.1111/brv.12174.

Morand-Ferron, J. (2017). Why learn? The adaptive value of associative learning in wild populations. *Current opinion in behavioral sciences, 16*, 73–79. https://doi.org/10.1016/j.cobeha.2017.03.008.

Nakatani, Y., Matsumoto, Y., Mori, Y., Hirashima, D., Nishino, H., Arikawa, K., & Mizunami, M. (2009). Why the carrot is more effective than the stick: Different dynamics of punishment memory and reward memory and its possible biological basis. *Neurobiology of learning and memory, 92*, 370–380. http://dx.doi.org/10.1016/j.nlm.2009.05.003.

Nöbel, S., Danchin, E., & Isabel, G. (2018). Mate-copying for a costly variant in *Drosophila melanogaster* females. *Behavioral Ecology, 29*(5), 1150–1156. https://doi.org/10.1093/beheco/ary095.

Pravosudov, V. (2022). Cognitive ecology in the wild — advances and challenges in avian cognition research. *Current Opinion in Behavioral Sciences. 45*, 101138. https://doi.org/10.1016/j.cobeha.2022.101138.

Raine, N., & Chittka, L. (2008). The correlation of learning speed and natural foraging success in bumble-bees. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 803–808. https://doi.org/10.1098/rspb.2007.1652.

Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, https://imagej.nih.gov/ij/, 1997–2018.

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rowe, C. & Healy, S.D. (2014). Measuring variation in cognition. *Behavioral Ecology, 25*(6), 1287-1292. https://doi.org/10.1093/beheco/aru090.

Sarin, S., & Dukas, R. (2009). Social learning about egg-laying substrates in fruitflies. *Proceedings of the Royal Society B: Biological Sciences, 276*, 4323–4328. https://doi.org/10.1098/rspb.2009.1294.

Shaw, R., MacKinlay, R., Clayton, N., & Burns, K. (2019). Memory performance influences male reproductive success in a wild bird. *Current Biology, 29,* 1498–1502. https://doi.org/10.1016/j.cub.2019.03.027.

Shettleworth, S.J. (2009). *Cognition, evolution, and behavior*. Oxford University Press.

Thornton, A. & Lukas, D. (2012). Individual variation in cognitive performance: Developmental and evolutionary perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367,* 2773–2783. https://doi.org/10.1098/rstb.2012.0214.

Webster, M., & Laland, K. (2017). Social information use and social learning in non-grouping fishes. *Behavioral Ecology 28*(6), 1547–1552. https://doi.org/ 10.1093/beheco/arx121.

Weissman, D., & Gray, D. (2019). Crickets of the genus *Gryllus* in the United States (Orthoptera: Gryllidae: Gryllinae). Magnolia Press.

Weissnitzer, J., Mangan, M., & Webb, B. (2008). Place memory in crickets. *Proceedings of the Royal Society B: Biological Sciences, 275.* 915–921. https://doi.org/10.1098/rspb.2007.1647.