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ORIGINAL ARTICLE

Wild non-eusocial bees learn a colour discrimination task in response to simulated predation events

Scarlett R. Howard[1]

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Abstract

Despite representing the majority of bee species, non-eusocial bees (e.g. solitary, subsocial, semisocial, and quasisocial species) are comparatively understudied in learning, memory, and cognitive-like behaviour compared to eusocial bees, such as honeybees and bumblebees. Ecologically relevant colour discrimination tasks are well-studied in eusocial bees, and research has shown that a few non-eusocial bee species are also capable of colour learning and long-term memory retention. Australia hosts over 2000 native bee species, most of which are non-eusocial, yet evidence of cognitive-like behaviour and learning abilities under controlled testing conditions is lacking. In the current study, I examine the learning ability of a non-eusocial Australian bee, *Lasioglossum (Chilalictus) lanarium*, using aversive differential conditioning during a colour discrimination task. *L. lanarium* learnt to discriminate between salient blue- and yellow-coloured stimuli following training with simulated predation events. This study acts as a bridge between cognitive studies on eusocial and non-social bees and introduces a framework for testing non-eusocial wild bees on elemental visual learning tasks using aversive conditioning. Non-eusocial bee species are far more numerous than eusocial species and contribute to agriculture, economics, and ecosystem services in Australia and across the globe. Thus, it is important to study their capacity to learn flower traits allowing for successful foraging and pollination events, thereby permitting us a better understanding of their role in plant-pollinator interactions.

Keywords Australia · Behaviour · Conditioning · Learning · Pollinators · Predation

Introduction

A large amount of research has focused on the learning abilities of eusocial bees. Honeybees (*Apis mellifera*) and bumblebees (*Bombus terrestris*) are among the most-studied bee species in terms of learning, memory, and cognition. For example, honeybees demonstrate evidence of both elemental (simple) and non-elemental (complex/relational) learning. Honeybees can discriminate between colours (Dyer and Arikawa 2014; Dyer and Neumeyer 2005; Dyer et al. 2008) and patterns (Dyer and Griffiths 2012; Efler and Ronacher 2000; Giurfa et al. 1999; Horridge 1997; Zhang and Srinivasan 1994), tasks which are generally considered elemental learning facilitated by associative mechanisms. Honeybees can perform more complex tasks including learning relational rules such as above vs. below (Avarguès-Weber et al. 2011), same vs. different (Giurfa et al. 2001), greater vs. lesser (Bortot et al. 2019a; Howard et al. 2018a), and smaller vs. larger (Avarguès-Weber et al. 2014; Howard et al. 2017a, b). They also demonstrate the acquisition of complex concepts such as maze navigation (Collett et al. 1993; Zhang et al. 1996, 2000), facial recognition (Avargues-Weber et al. 2018; Avarguès-Weber et al. 2010b; Chittka and Dyer 2012; Dyer et al. 2005), abstract character use (Howard et al. 2019d; Zhang et al. 1999), counting (Chittka and Geiger 1995; Dacke and Srinivasan 2008), arithmetic (Howard et al. 2019a, b), and quantity discrimination (Howard et al. 2018a, 2019c, 2020).

While learning and memory tasks are comparatively understudied in non-eusocial bees, previous work shows evidence of learning abilities in a number of solitary bee species. *Osmia lignaria* (Amaya-Marquez and Wells 2008), *Xylocopa virginica* (Dukas and Real 1991), *Heriades truncorum* (Chittka et al. 1992), and *Osmia rufa* (Menzel et al. 1988) can learn important colour discrimination tasks.

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✉ Scarlett R. Howard
s.howard@deakin.edu.au

[1] Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, VIC, Australia

Eucera sp. appears to learn an ecologically relevant counting task (Bar-Shai et al. 2011), where flower nectaries are counted as bees feed to avoid return visits to empty nectaries. *Osmia caerulescens* and *Osmia leaiana* (Loukola et al. 2020) learn to avoid or visit nests based on abstract characters representing parasitized or non-parasitised nesting sites. *Xylocopa micans* demonstrates learning of flower colour, showing more visits to rewarding flowers (higher in nectar concentration or volume) in less than six trials (Perez and Waddington 1996). *X. micans* also demonstrates the use of colour and location learning when foraging on vertical inflorescences of three artificial flowers, where just one contained nectar. Although they preferred to use colour cues, in the absence of colour information, *X. micans* could use spatial information (Orth and Waddington 1997). Colour and spatial information of rewarding flowers were learnt within five foraging bouts by *X. micans*, suggesting rapid visual and spatial learning (Orth and Waddington 1997; Somanathan et al. 2019). Additionally, other ecologically relevant learning tasks have been demonstrated in the nocturnal *Xylocopa tranquebarica* which can visually learn coloured landmarks for nest recognition (Somanathan et al. 2008).

Bees are a model species for testing learning, cognition, and memory in invertebrates (Avarguès-Weber and Giurfa 2013; Chittka 2017; Dyer 2012; Srinivasan 2010). Research has shown that the method of conditioning impacts the learning ability of bees. The major types of differential conditioning, where two or more stimuli are presented to the bee simultaneously, are appetitive differential conditioning, aversive differential conditioning, and appetitive-aversive differential conditioning. Appetitive differential conditioning involves rewarding a correct choice of stimulus while providing no outcome for an incorrect choice. Aversive conditioning involves a punishment for an incorrect stimulus choice and no outcome for a correct choice. Finally, appetitive-aversive differential conditioning involves providing a reward for a correct choice and a punishment for an incorrect choice. Using appetitive-aversive differential conditioning is known to improve learning in bees during visually and conceptually difficult tasks such as fine colour discrimination (Avarguès-Weber et al. 2010a; Chittka et al. 2003) and quantity discrimination (Howard et al. 2019c). While appetitive-aversive and appetitive differential conditioning can be used in free-flying bee experiments [for examples, see Avarguès-Weber et al. (2014); Avarguès-Weber et al. (2015); Avarguès-Weber et al. 2011; Bortot et al. (2019a, b); Chittka and Geiger (1995); Dyer and Chittka (2004); Dyer et al. (2005); Garcia et al. (2018); Giurfa et al. (2001); Howard et al. (2019c, d); Perry and Barron (2013)], aversive learning is used in experiments where bees are constrained in harnesses or closed arenas (Marchal, 2019; Nouvian and Galizia 2019; Vergoz et al. 2007). The type of aversive outcome/punishment can include mild electric shocks (Marchal et al. 2019; Nouvian and Galizia 2019; Vergoz et al. 2007) or simulated predation events (Jones and Dornhaus 2011; Zhang and Nieh 2015). In the current study, I employ the latter. Past work has shown that simulated crab-spider predation events (Fig. 1a) are successful as an aversive outcome in learning tasks related to flower choice and colour discrimination in eusocial bee species (Ings et al. 2012; Ings and Chittka 2008, 2009; Jones and Dornhaus 2011; Wang et al. 2013; Zhang and Nieh 2015).

In the current study, I tested a widespread Australian native bee, *Lasioglossum (Chilalictus) lanarium*, for its ability to learn a simple colour discrimination task. I presented bees with two colours, known to be easily discriminated by honeybee vision in a previous study (Howard et al. 2019b). Bees were trained using aversive differential conditioning, with a simulated predation event acting as the aversive outcome to an incorrect choice. The current study aims to aid in bridging the gap between learning and cognitive studies on eusocial and non-eusocial bees and demonstrates how non-eusocial bees may learn important plant-pollinator signals such as flower colour to find rewarding flowers and avoid predators.

Methods

Study species and collection

The native Australian bee, *L. lanarium* (family Halictidae), was used in this study. Halictids are short-tongued bees with most species being ground-nesting and a few burrowing into rotten branches, logs, or stumps (Houston 2018). *Lasioglossum* bees are found across Australia (Danforth and Ji 2001). Specifically, *L. lanarium* is a widespread (Atlas of Living Australia website), ground-nesting bee species which forages on multiple flowering plant species. *L. lanarium* nest in communal aggregations of females (Houston 2018).

Male and female *L. lanarium* were collected in south-east Melbourne, Australia (near the latitudes and longitudes of − 37.858, 145.0952 and − 37.871, 145.187 in residential gardens) on the days of experiments during November 2020. The sex of bees was not determined for all individuals; thus these data were not included in the analysis. Bees were captured in small transparent plastic vials with air holes, transported to a testing arena in a dark bag, and behavioural assays were conducted within 24 h of capture during daylight hours.

The transport of the bees to the experimental area while in the vial in a dark opaque bag appeared to prevent escape behaviour enough so that when released from the vial, they did not exhibit an escape response but still moved around the arena with motivation to approach the stimuli (Online Resource 1). Different individuals exhibited different levels

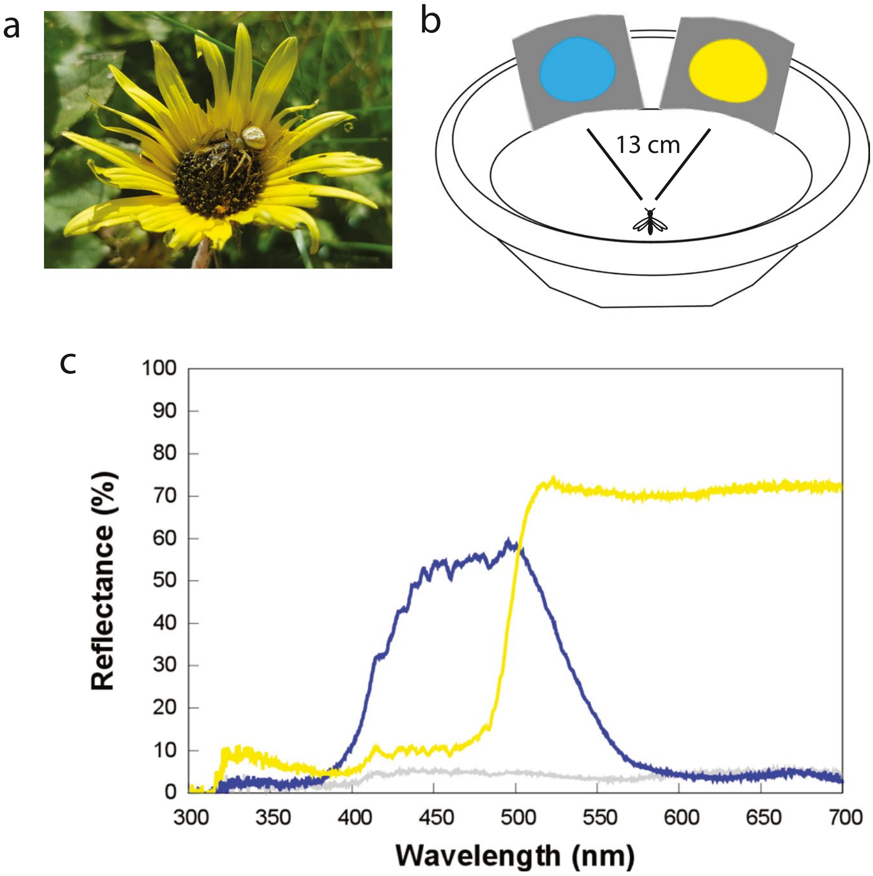

Fig. 1 **a** Crab-spider preying on a *L. lanarium* bee. **b** Arena with representations of stimuli and bee position. **c** The percentage of reflected radiation plotted against wavelength for the grey stimulus background (grey), the yellow stimulus (yellow), and the blue stimulus (navy)

of activity and escape behaviour following capture but did not try to escape at the beginning of the experiments.

Apparatus

The circular arena was constructed of white plastic 16 cm in diameter and 4.5 cm in height (Fig. 1b). The bee was released at one edge of the arena when presented with two stimuli at the other edge. Bees were individually tested. Experiments were conducted under natural diffuse daylight conditions.

Stimuli

Salient blue and yellow circles on a background of neutral grey were used as the stimuli (Fig. 1b, c). Stimuli were 6 × 6 cm (36 cm^2) laminated cards presenting the coloured circle of 10 cm^2 in surface area. The colours are easily discriminable by bees, which is demonstrated in a previous study on honeybees (Howard et al. 2019b) and based on current knowledge of bee colour vision (Briscoe and Chittka 2001; Chittka 1992; Dyer and Arikawa 2014). The reflectance spectrum of each colour (grey background and target colours) was measured with a spectrophotometer fitted with quartz optics and a PX-2 pulsed xenon UV–visible radiation source (USB 2000 +, Ocean Optics, Dunedin, FL, USA) that closely matches the spectral profile of typical daylight illumination. The spectrophotometer was attached to a computer running SpectraSuite software 2011. The results of these measurements are plotted in Fig. 1c.

Training and testing procedure

Individual bees were placed 13 cm away from the two stimuli presented. Bees were transported in and out of the arena and manipulated around the experimental area on a toothpick. Once bees were placed into the arena for the first time, a choice was recorded for either the yellow or blue stimulus. This first choice acted as preference test or ‘pre-test’; bees would then be trained on the opposite colour to what they had first chosen. For example, if a bee preferred blue on the first choice, they would then be trained to avoid the blue stimulus, similar to previous work with honeybees (Buatois et al. 2018). During the preference test, $n = 21$ bees chose the yellow stimulus and thus were trained to avoid the yellow stimulus, and $n = 19$ bees chose the blue stimulus and thus were trained to avoid the blue stimulus. The pre-test was necessary as recent evidence has shown *L. lanarium* bees have colour preferences (Howard et al. 2021). To demonstrate the motivation of bees and the attraction to stimuli, a video of a pre-test is included in Online Resource 1.

Bees underwent ten aversive training trials. Then ten unreinforced test choices (no outcomes for a correct or incorrect choice) were conducted to determine whether they had learnt to avoid the incorrect stimulus, similar to unreinforced tests in other bee behaviour studies (Howard et al. 2019b, c, d; Howard et al. 2020, 2021). During aversive differential conditioning, bees were placed at the starting point and then walked towards a stimulus and made a choice (usually within 1 min of being placed into the arena). If bees chose incorrectly, they would receive an aversive outcome — a simulated predation event. If bees chose correctly, there was no outcome.

The simulated predation event involved gently squeezing the bee's abdomen with forceps when it climbed onto the incorrect stimulus. This procedure simulates the attack of a crab spider, a predator of *L. lanarium* (personal observation; Fig. 1a). This method or similar has been successfully used previously with forceps (Jones and Dornhaus 2011; Zhang and Nieh 2015) and robotic crab spiders (Ings et al. 2012; Ings and Chittka 2008, 2009; Wang et al. 2013). Bees were provided breaks of 10–30 s between trials.

If bees exhibited escape behaviour following the aversive outcome for an incorrect choice, polyethylene film was placed over the arena which prevented escape but allowed both visible light and UV light to pass through. The cover still allowed the aversive outcome to be applied due to the plastic film's flexibility.

Statistical analysis

To determine if bees demonstrated significant learning during training, data from the ten aversive differential conditioning trials were analysed with a generalized linear mixed-effects model (GLMM) with a binomial distribution using the 'glmer' package within the R environment for statistical analysis. I first fitted a full model with choice as the categorial response variable with two levels (correct; incorrect), individual trial number as a continuous predictor (1–10), colour as a categorical predictor with two levels (yellow; blue), and an interaction between trial and colour as a predictor. Subject (bee ID) was included as a random factor to account for repeated choices of individual bees.

To determine whether bees learnt to discriminate between yellow vs. blue stimuli, I analysed the test data by employing a GLMM with a binomial distribution including categorial response variable with two levels (correct; incorrect), individual test choice number as a continuous predictor (1–10), colour as a categorical predictor with two levels (yellow; blue), and an interaction between trial and colour as a predictor. Subject was included as a random factor to account for repeated choices of individual bees. The proportion of choices for the correct colour (MPCC) recorded from the tests was used as the response variable in the model. The Wald statistic (z) tested if the mean proportion of correct choices recorded from the test, represented by the coefficient of the intercept term, was significantly different from chance expectation, i.e. H_0: MPCC = 0.5.

The models were estimated using the routine 'glmer' available as part of the 'lme4' package written for the R statistical language, run in R version 4.0.3 (Bates et al. 2014; R Core Team 2020).

Results

Training

The analysis from the full model including trial (continuous), colour (categorical with two levels: blue; yellow), and an interaction between the two predictors showed no effect of the interaction ($z = -0.846$, $P = 0.398$); thus the interaction term was removed. The subsequent reduced model showed no effect of colour ($z = 1.744$, $P = 0.0812$), but an effect of trial ($z = 3.277$, $P = 0.001$). The simplified model excluding colour showed a significant effect of trial on bee performance ($z = 3.265$; $P = 0.001$). See Fig. 2a.

As the P value for the effect of colour was < 0.100 but > 0.050, I compared the AIC values of the model including and excluding colour (both models excluding the interaction effect). The model including colour had an AIC value of 543.700. The simplified model excluding the effect of colour had an AIC value of 544.700; thus the model of best fit included colour and showed that bees learnt the task over the ten aversive conditioning trials with an overdispersion (OV) value of 1.349 showing that the training data was slightly overdispersed but within a reasonable range to conduct the analysis.

Testing

Each bee underwent ten unreinforced choices during a learning test to determine if they had learnt the task of yellow vs. blue (Fig. 2b). There was no significant difference between bees trained to avoid the yellow or blue stimulus ($z = 0.988$; $P = 0.323$); therefore the data were pooled for analysis.

Bees discriminated between blue and yellow stimuli during the learning test following the ten training choices at a level of 62.75% (confidence intervals [CIs] = 0.557, 0.690; $z = 5.043$; $P < 0.001$; $n = 40$; Fig. 2b). The data collected was slightly overdispersed (OV = 1.32) but still within a reasonable range to conduct the analysis.

When examining only the first choice of bees during the test (thus without a subject as a random term as there were

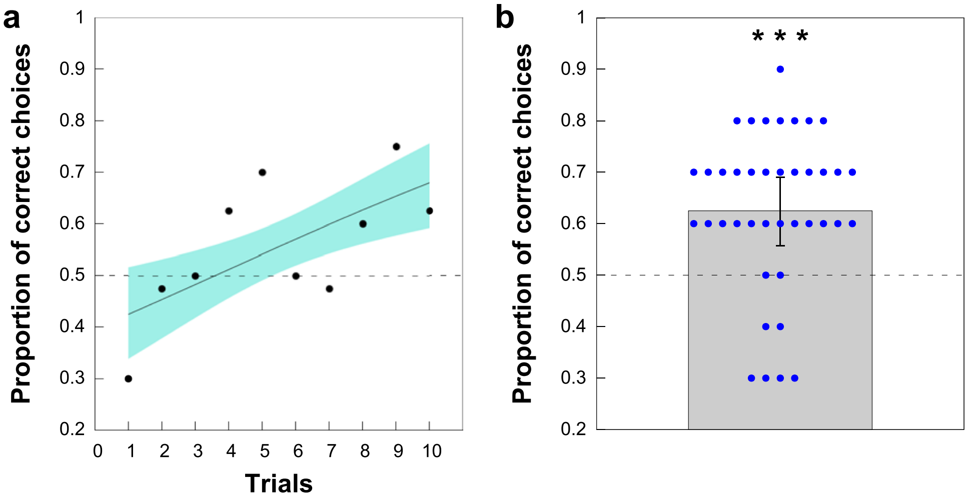

Fig. 2 Results of the training and testing phases. Left panel (**a**) shows the performance of bees during the learning phase. The solid black line represents a function describing the learning phase of $n = 40$ bees as modelled by a generalized linear mixed-effect model (GLMM). Shaded area indicates the ± 95% confidence intervals (CIs) of correct choices for the bees (turquoise). The increase in learning performance was significant. Dashed line at 0.5 indicates chance level performance. Black circles show the mean performance of all bees ($n = 40$) for each trial. Right panel (**b**) shows the mean proportion of correct choices [mean ± 95% confidence intervals (CIs)] by *L. lanarium* during all ten choices during the unreinforced test. Broken black line shows chance expectation at 0.5. Blue circles indicate the raw data from each individual bee ($n = 40$) as a bee-swarm plot. Significance from chance level performance is indicated by *** ≥ 0.001

no repeated measures in the model), bees chose the correct stimulus at a level of 75.00% (CIs = 0.595, 0.860; $z = 3.009$; $P < 0.003$; $n = 40$), which is consistent with what was found when bees underwent all ten unreinforced choices in the test.

Discussion

The current study presents evidence that a wild non-eusocial bee can learn the elemental task of colour discrimination using aversive differential conditioning when colours are saliently different. Colour discrimination is a potentially useful capacity in *L. lanarium*'s natural environment. Bees are known to use different signals or cues from flowers to choose which flowers to visit. These signals and cues include scent (Raguso 2008), colour (Giurfa et al. 1995), shape (Howard et al. 2018b; Lehrer et al. 1995), size (Martin 2004), quantity of flowers (Howard et al. 2020), and/or symmetry (Giurfa et al. 1996); thus bees must learn which flowers to visit based on these traits. Colour signalling by flowers appears to be the main plant-pollinator communication channel in studies from around the world (Barth 1985; Mitchell et al. 2009; Sargent and Ackerly 2008), and so colour discrimination learning is an important behaviour to examine in understudied non-eusocial bees. The ability of *L. lanarium* to discriminate between two colours suggests that in a natural foraging situation, this species may learn to visit rewarding flower colours, avoid non-rewarding flower colours, or even learn to avoid flower colours which host crab-spiders (Fig. 1a), similar to findings in past studies (for example, Jones and Dornhaus 2011).

A few studies have directly compared the learning abilities of eusocial and solitary bees. These studies suggest that while there are differences between learning in eusocial and non-eusocial bees, fundamental aspects of learning are shared between the two groups. In a colour discrimination experiment, *A. mellifera* (eusocial) learnt more quickly than *O. lignaria* (solitary) in the case of discriminating between flower colour morphs (Amaya-Marquez and Wells 2008). The eusocial bumblebee, *B. bimaculatus*, and the solitary carpenter bee, *X. virginica*, were compared for learning of flower colours. While *B. bimaculatus* demonstrated higher rates of learning, both species had similar levels of overnight memory retention (Dukas and Real 1991). In the field, it appears that *B. terrestris* (eusocial) may have a more exact counting strategy for flower nectaries than *Eucera* sp. (solitary) (Bar-Shai et al. 2011). Thus, in these few comparisons, eusocial bees appear to learn more quickly (Amaya-Marquez and Wells 2008) or demonstrate higher rates of learning then non-eusocial solitary bees (Dukas and Real 1991), but more research is needed to determine whether this trend is widespread or restricted to a few species comparisons.

Non-eusocial wild bees are important pollinators in terms of agriculture, economics, and ecosystem services in Australia and across the globe (Bell et al. 2006; Bray 1973; Heard 1999; Hogendoorn et al. 2010, 2007, 2006, 2000; Hogendoorn and Keller 2012; Kleijn 2015); however they are threatened by a number of anthropogenic activities such as land-clearing, habitat loss and fragmentation, urbanisation, pesticide and insecticide use, climate change, disease, fire, and invasive species introductions (Batley and Hogendoorn 2009; Brown and Paxton 2009; Goulson et al. 2015; Herrera 2020; Mallinger et al. 2017; Owens et al. 2020; Potts et al. 2010; Santos et al. 2020). The biggest threat to Australian native bees remains a lack of information, knowledge, and expertise (Batley and Hogendoorn 2009; Sands 2018; Taylor et al. 2018). Thus, the current study and further research should work towards filling this gap in knowledge and developing robust frameworks to study non-eusocial wild bees. Future work should aim to determine effective ways to test learning and memory in non-eusocial bees using both aversive and appetitive conditioning and develop testing of more complex learning tasks for comparison with eusocial bees. As non-eusocial bees are important but comparatively understudied pollinators, efforts to examine their behaviour and foraging decisions are imperative.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00114-021-01739-9.

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Author contribution SRH performed data collection, analysis, and wrote the manuscript.

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Data availability All data generated or analysed during this study are included in this published article [and its supplementary information files].

Code availability Available upon request.

Declarations

Ethics approval All animal care was in accordance with institutional guidelines. Formal ethics approval was not required for invertebrate behavioural testing.

Conflicts of interest The author declares no competing interests.

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