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Intra-specific differences in cognition: bumblebee queens learn better than workers

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Species' cognitive traits are shaped by their ecology, and even within a species, cognition can reflect the behavioural requirements of individuals with different roles. Social insects have a number of discrete roles (castes) within a colony and thus offer a useful system to determine how ecological requirements shape cognition. Bumblebee queens are a critical point in the lifecycle of their colony, since its future success is reliant on a single individual's ability to learn about floral stimuli while finding a suitable nest site; thus, one might expect particularly adept learning capabilities at this stage. I compared wild *Bombus vosnesenskii* queens and workers on their ability to learn a colour association and found that queens performed better than workers. In addition, queens of another species, *B. insularis*, a cuckoo species with a different lifecycle but similar requirements at this stage, performed equally well as the non-parasitic queens. To control for differences in foraging experience, I then repeated this comparison with laboratory-based *B. impatiens* and found that unmated queens performed better than workers. These results add to the body of work on how ecology shapes cognition and opens the door to further research in comparative cognition using wild bees.

1. Introduction

Cognitive traits are shaped both by natural selection and affected by an individual's experience. Determining the ecological factors that shape cognition often involves making inter- and intra-specific comparisons [1–4]. While comparisons with laboratory-reared animals allow for experience to be tightly controlled, to understand the evolution of cognitive traits, it is necessary to measure cognition in wild animals [5,6]. Honeybees *Apis* and bumblebees *Bombus* have been models of learning for decades [7,8], with the vast majority of behavioural work focused on one life stage and caste: the female foragers. As floral generalists, foragers can learn associations with a broad variety of stimuli and rewards [8]. However, bumblebee colonies go through a number of life stages (figure 1) and include castes with different natural histories and cognitive requirements. Since learning carries both an energetic cost in the short term [9] and possible fitness trade-offs [10], we might expect learning abilities to differ between castes depending on ecological requirements. Variation in learning performance has been found both within and between bumblebee colonies [11,12], yet castes aside from foragers are rarely studied. One stage where we might expect a particularly critical need for learning is for foraging queens: after emerging from hibernation, their future reproductive success rides on the ability of this single individual to forage efficiently during the initial stages of colony founding [13]. While foragers are known to be adept at learning associations, the consequences of making a mistake or foraging sub-optimally are less critical than for a foraging queen, since foragers can rely on their colony. Similar patterns are seen between honeybee and bumblebee foragers, where honeybee

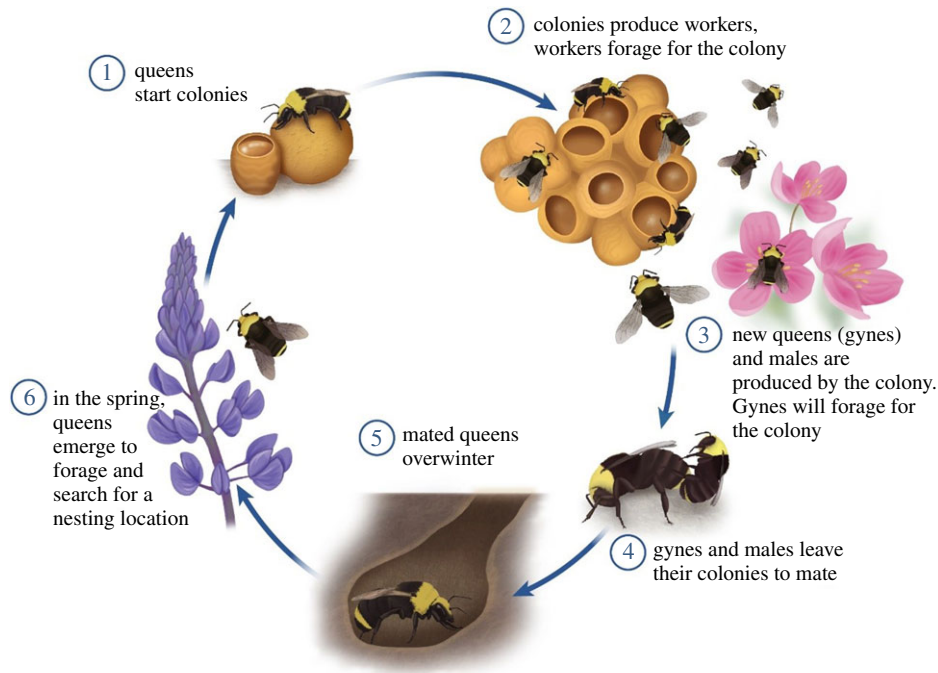


Figure 1. The typical lifecycle of a bumblebee colony. In the field experiment, foraging queens that had not yet started colonies (stage 6) were compared to foraging workers (stage 2) in their ability to learn a colour association. In the laboratory-based experiment, unmated queens and workers were compared at the same time (stage 3) and with the same experience. Illustration credit: Ann Sanderson <https://www.annsciart.com/>.

workers can ‘afford’ to make more mistakes because they are part of a larger colony [14]. Despite foraging queens being a critical point in the bumblebee lifecycle, we know almost nothing about their cognitive abilities (but see [15,16]).

Using wild-caught *Bombus vosnesenskii*, I compared foraging queens and workers in their ability to learn a colour association. Associative learning of floral cues is critical for foraging bumblebees and may correlate with colony fitness ([12] but see [17]). I expected that queens would be better at learning, given the potential for errors to carry a particularly high cost for them. I also compared *B. vosnesenskii* to queens of another species: *Bombus insularis*. This species is a brood-parasitic ‘cuckoo’, which does not form its own colony, but instead usurps a colony from other bumblebee species [18]. As such, this species does not produce workers, only queens and males which are raised by the parasitized colony. Despite these differences in their lifecycle, *B. insularis* queens experience similar ecological pressures to non-cuckoo queens to be highly efficient foragers, and as such I expected that they would perform equally well at a learning task. To control for the effects of foraging experience, I then compared unmated queens (gynes) to foragers at the same stage of the colony lifecycle in the laboratory, using captive-reared *Bombus impatiens*.

2. Methods

(a) Field experiment

Field data were collected between April and July 2020 at sites in the Great Basin Desert near Reno, Nevada, hereafter ‘desert sites’ and a montane meadow and mixed conifer forest (Dog Valley, California), hereafter ‘meadow sites’. Desert-bees were active (and therefore tested) before meadow-bees, and queens before workers (electronic supplementary material, figure S1). Within the desert sites, *B. vosnesenskii* and *B. insularis* queens were collected from *Balsamorhiza hookeri*, *Prunus andersonii* and *Salvia dorii*, and workers from *Penstemon palmeri*, *Lavandula angustifolia*, *Cytisus scoparius*

and *Carduus nutans*. At the meadow sites, queens were collected from *Wyethia mollis*, *Cirsium scariosum*, *Penstemon rydbergii*, *Penstemon heterodoxus* and *Vicia* sp. and workers from *Lupinus* sp.

Queen ($n = 56$) and worker ($n = 45$) *B. vosnesenskii* bumblebees were netted on flowers at desert and meadow sites; *B. insularis* ($n = 16$) were only found at desert sites. No *B. vosnesenskii* queens were carrying pollen and were presumed to be early-season queens which had not yet started colonies. They were transferred to plastic ‘preference tubes’ ($1 \times w \times h$: $2.5 \times 2.5 \times 15$ cm) with two holes at each end through which stimuli could be inserted (figure 2a). Bees were left for approximately 3 h, 15 min prior to testing to allow them to habituate to the tubes and become motivated to forage. Bees were initially tested for their sucrose responsiveness (electronic supplementary material), since this has previously been associated with learning performance in honeybees [19,20]. They were then trained to learn a colour association using the ‘Free-Moving Proboscis Extension Response’ (FMPER) ([21,22], see also <https://methodsblog.com/2017/09/21/bee-cognition/>). Each bee was trained via differential conditioning where either a yellow or blue strip of card (Bazzill Cardstock, USA) was rewarding. Each bee was first given two ‘no choice’ trials, where they were presented with the rewarding colour (CS+) dipped in 50% (w/w) sucrose, followed by the unrewarding colour (CS-) (dipped in water). In each case, the strip was presented to the bee’s antennae, and it was allowed to drink for 3 s (in the case of the CS-, bees often did not extend their proboscis after antennating, or only briefly probed the strip). These two ‘no choice’ trials served to motivate bees to partake in the ‘choice’ trials. For the ‘choice’ trials (five total), I presented bees with both stimuli simultaneously (figure 2a). Their choice was recorded as either ‘correct’ or ‘incorrect’, depending on whether they chose the CS+ or CS- first. Once the bee made contact with the strip using its antennae or proboscis, it was given 3 s to drink/sample the solution. This strip was then removed and the bee was given the other strip for 3 s after making contact with it; in later trials bees would often walk away from the CS- without making contact and in these cases, the strip was removed after the bee rejected it. Eight bees were tested within

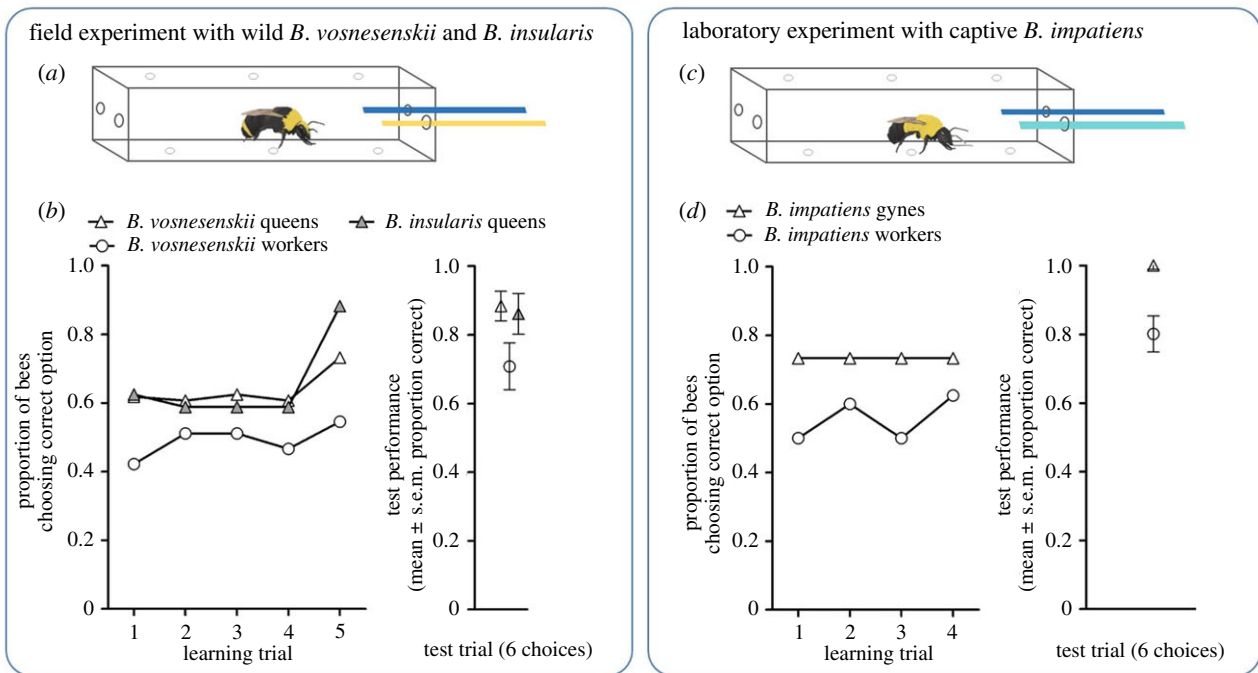


Figure 2. (a) Diagram of the set-up for field-caught bees. (b) *B. vosnesenskii* queens ($n = 56$) were better at learning than workers ($n = 45$) across learning trials and in the unrewarded test phase. *B. insularis* queens (a cuckoo species; $n = 16$) performed as well as non-parasitic queens. (c) Diagram of the set-up for laboratory-tested bees. (d) *B. impatiens* gynes ($n = 15$) performed better than workers ($n = 16$) at learning the colour discrimination. Note that in both experiments, bees had already encountered the stimuli in two 'no choice' trials prior to the first learning trial.

a block by testing bees sequentially within each trial, resulting in inter-trial-intervals of approximately 10 min for each bee. After the fifth trial, I gave bees 10 'test' trials where both coloured strips were unrewarding (contained water); these were conducted in quick succession to prevent loss of motivation. For each test trial, the colour of strip that the bee first approached (antennated or exhibited proboscis extension towards) was recorded. Since many bees stopped responding before the 10 test trials were complete, only the first six were analysed.

(b) Laboratory experiment

Workers ($n = 16$) and gynes ($n = 16$) were taken directly from a single commercially purchased colony of *Bombus impatiens* (Kopert, USA) which had been given access to a white-wicked feeder of 30% (w/w) sucrose. Bees were placed in preference tubes for approximately 2 h, 40 min prior to training. Pilot trials showed that following the same training protocol as the field experiment led to bees learning too readily to make comparisons (all bees performed at 100% correct in the test). As such, the protocol was adapted to make the discrimination more difficult: a lighter blue (hereafter 'aqua') was used in place of the yellow stimulus and the choice trials were reduced from five to four. Bees were given six choices in the test phase. Aside from these adjustments, the learning and test trials were conducted in the same way as for the field experiment.

(c) Data analysis

All data were analysed in R v. 4.0.5 using binomial GLMMs in the nlme package [23] with learning performance (correct/incorrect) as the response variable. The effects package [24] was used to visualize interactions and carry out post hoc tests. For details of statistical analyses, see electronic supplementary material.

3. Results

(a) Field experiment

At meadow sites, queen *B. vosnesenskii* were more responsive to sucrose than workers, while there was no difference at desert

sites. *B. insularis* were much more responsive to sucrose than *B. vosnesenskii* queens and workers (electronic supplementary material, figure S2). At both desert and meadow sites, *B. vosnesenskii* queens learned better than workers (learning trial: $z = -3.029$; $p = 0.002$; test trial: $z = -4.846$; $p < 0.0001$; figure 2b). Bees did not significantly improve across learning trials ($z = 1.556$; $p = 0.120$). Across the learning trials, bees trained to yellow performed better ($z = 4.161$; $p < 0.001$; electronic supplementary material, figure S3), and there were no differences between desert- and meadow-caught bees ($z = 0.281$; $p = 0.216$). In the test trials, an interaction was detected where at the meadow site, there appeared to be stronger colour preferences: bees trained to yellow performed better than bees trained to blue, while this effect was weaker at the desert site (rewarding colour \times location: $z = -2.728$; $p = 0.006$; location: $z = 3.576$; $p < 0.0001$; rewarding colour: $z = 5.082$; $p < 0.0001$; electronic supplementary material figure S4).

Bombus insularis queens performed as well as *B. vosnesenskii* queens (i.e. no difference in either the learning trial: $z = 0.449$; $p = 0.653$, or the test trial: $z = -1.442$; $p = 0.149$; figure 2b).

(b) Laboratory experiment

Results from a laboratory-based assay using *Bombus impatiens* were similar to the field experiment. There was a strong trend for gynes to perform better than workers across the learning trials ($z = -1.916$; $p = 0.055$) and gynes outperformed workers in the test phase, with all but one gyne choosing correctly 100% of the time ($z = -3.218$; $p = 0.001$). The proportion of bees choosing the correct option did not increase across the successive trials ($z = -0.078$ $p = 0.938$). A colour preference was seen in the learning trials, where bees were more likely to choose blue than aqua ($z = 3.018$; $p = 0.003$); in the test phase, colour preferences were not evident ($z = 0.514$; $p = 0.607$), likely because of the high performance across both groups.

4. Discussion

Social insects have served as models for cognition for decades [8,25], yet the vast majority of the work has focused on foragers. Here, I found that the cognition of wild queen bumblebees varied from that of workers in a manner that would be expected by their ecological role: queens of both a eusocial and parasitic species were better at learning associations with a floral (colour) cue and nectar reward, than foragers. This was the case for both wild-foraging bees, as well as for captive bees with limited foraging experience that were tested at the same colony stage. The finding that despite differences in sociality, eusocial and parasitic queens did not differ to each other indicates that their learning abilities (or at least, those measured in the current experiment) may reflect queens' need to forage effectively at this stage rather than other differences in their ecologies.

The present results agree with those from a free-flying assay using laboratory-reared *B. terrestris*, where three queens performed better in learning a colour discrimination than the foragers from their colonies [15] and work with domesticated honeybees, where 5-day-old unmated queens performed better than age-matched workers in an olfactory learning assay [26]. That bumblebee queens are better at learning associations than foragers may be explained by mistakes at this stage carrying relatively large fitness consequences. It is also possible that variation in learning performance among foragers is adaptive, since apparent errors can lead to the discovery of novel food sources [27] which may benefit the colony as a whole. Finally, it may be the case that the higher learning performance of queens does not reflect better learning per se, but rather differences in sensory sensitivity. For example, queens have both larger bodies and eyes, likely with more ommatidia [28–30], and as such may be better able to differentiate the coloured strips. Determining the underlying mechanism (e.g. differences in the brain versus peripheral sensory regions) would help inform function. Whether queen and worker bumblebees differ in their brain morphology has not, to my knowledge, been investigated (but see [31]). However, in related systems (sweat bees: [32,33]; paperwasps: [34–36]), queens and workers vary in features of their mushroom bodies, regions of the brain associated with learning and memory [37].

In the present study, commercially reared *B. impatiens* learned more readily than the wild-caught bumblebees and thus had to be given a more difficult discrimination task. While this may reflect species differences, a more likely explanation is that the colour stimuli used were more salient to captive bees, since they were largely naive to colour in a foraging context. Such a role for prior experience was indicated by the behaviour of the bees wild-caught from meadow

sites. These bees had yellow colour biases in the learning protocol, which may be explained by a large number of yellow flowers (*Wyethia mollis*) that they were seen foraging on in this area.

Cognition has been shown to vary with social insects' foraging role in a few other contexts. Honeybee nectar-foragers typically have higher sucrose response thresholds than other roles such as guards, undertakers and pollen-foragers [38–40]. This can be explained by it being beneficial for nectar-foraging bees to be the most discriminatory in their nectar preferences. Previous work has also shown that honeybees that are more responsive to a given concentration of sucrose are better at learning associations [19,20]. This relationship is inconsistent with the present results, since learning performance was not explained by sucrose responsiveness. Beyond foragers, a few studies have addressed male bee cognition and generally found equal performance to foragers [22,41,42]. This may also be expected by their ecological role: while males do not forage for the colony, they still need to learn floral associations while foraging for themselves and mate-searching for queens [22].

The queen stage of the bumblebee lifecycle has been largely neglected when it comes to cognition, likely because it can be practically difficult to replicate in a laboratory environment, and since wild-foraging queens can be challenging to test in large numbers in the field. Moving forward, the simple and non-lethal tools used here open the door to future research using this system [21]. For example, the comparison of other cognitive abilities (e.g. spatial), as well as learning across multiple modalities (e.g. olfactory), would inform how cognitive traits have been shaped in queens relative to their workers. Additionally, queens go through dramatic changes in their physiology throughout their lifecycle. While they have a critical need for learning capabilities at the start of their lifecycle, once they develop their ovaries and produce foragers, they cease foraging, solely focusing on egg-laying [13]. Variation in cognition associated with breeding state (or season) have been studied in vertebrates [43–46], but rarely investigated in invertebrates, although changes in brain morphology across reproductive state point to associated differences in cognition ([47,48], see also [49]).

Data accessibility. Data are published in the Dryad Digital Repository [50].

Competing interests. I declare I have no competing interests.

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