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OUTLOOK

Bumblebees show capacity for behavioral traditions

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Summary

A new study shows that bumblebees learn socially, and this resulted in a novel behavior becoming dominant across a group. These findings highlight the opportunity going forward to use social insects to address how simple cognitive mechanisms can underpin the development of complex behavioral phenomena.

Keywords Culture · Social learning · Associative learning

"Culture", defined as persistent behavioral norms within a group, created through the spread of information socially, is often hailed as a landmark of human society. The study of culture in non-human animals has garnered recent interest, including experimental demonstrations of how cultural norms can arise in wild primate and bird populations. A recent study (Bridges et al., 2023) shows that within bumblebee groups too, a novel behavior can spread via social learning, resulting in a dominant behavior. This result presents the opportunity to use bees to examine the cognitive mechanisms underlying the establishment of behavioral traditions.

Bridges et al. trained bees to one of two solutions to a "puzzle-box" feeder, requiring individuals to push a blue or red tab to gain a sucrose reward. Each solution was equally difficult, resulting in the same reward. "Demonstrator" bees were trained to perform one of the two variants ("red" or "blue"). "Observer" colonies were then given access to puzzle-boxes with demonstrators, allowing the behavior to spread throughout the group via social learning. In Experiment 1, four colonies, or replicates (two red, two blue), were each given access to eight puzzle-boxes in an arena, each containing a single demonstrator. Two control colonies were given the same puzzle-boxes without a demonstrator. Fourteen bees from the experimental colonies learned to open the feeder, nearly always in line with the demonstrated color, whereas only one control bee learned. To determine if control bees simply needed more time to learn, Experiment 2 lasted twice as long as Experiment 1, using one red, one blue, and two control colonies. Here, the highest number of learners (nine) was in one of the controls, while only four bees in each of the red and blue colonies learned.

Taken together, these experiments show that social learning can facilitate information spread, in line with previous work (Leadbeater & Chittka, 2007). The authors suggest that their findings demonstrate the potential for novel behavior to arise via genetic assimilation of learned behavior (the Baldwin effect). While an interesting idea, this conclusion would need further experiments, specifically showing that behaviors are genetically transmitted, rather than remaining plastic. More generally, linking cognition to fitness is no easy task, and recent work shows that even a seemingly advantageous cognitive trait like working memory can have a positive or negative relationship with bees' foraging efficiency depending on environmental conditions (Pull et al., 2022).

In a third experiment, Bridges et al. introduced both variants (two red-, two blue-trained demonstrators) at the same time, to determine if one variant would become dominant. Two observer colonies were attached to an arena, with twice the number of puzzle-boxes as before, to encourage a greater number of foragers. The experiment was repeated twice. At the end of the first iteration, most observer bees performed the red variant, whereas at the end of the second (using new colonies), most performed the blue variant. These results show that, in theory, when variants have equal payoffs, either one can prevail, despite a seeming blue color preference (control bees that solved the puzzle-box generally chose blue). The convergence on a single strategy was not driven by individuals changing their preferences to "conform," but rather new learners were more likely to adopt the preference of the majority.

That bumblebees learned more readily with demonstrators and that this led to a dominant behavior presents the opportunity to examine the cognitive mechanisms that may underpin

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the development of behavioral traditions. Previous work with bumblebees has shown that social learning can be explained by second-order conditioning (Leadbeater & Dawson, 2017), where individuals initially learn that other bees (conditioned stimuli/CS1) predict sucrose rewards (unconditioned stimuli/US+) when encountering conspecifics on feeders. Conspecifics (CS1) then become paired with a second conditioned stimulus (CS2; in this case, a blue or red tab). This may in part explain how bees learned in the current experiment, although there was also the opportunity for individual learning (i.e., via first-order conditioning), as observers could land next to a demonstrator feeding from a puzzle-box and gain the reward themselves. Bridges et al. raise the possibility of local enhancement versus stimulus enhancement as processes by which bees learned, and past work suggests that both may be at play: naïve bees may be first drawn to conspecifics as salient stimuli (local enhancement). After gaining rewards themselves, observers likely learn that a tab-stimulus predicts reward and generalize that response to all tabs of that color (stimulus enhancement). In cases where there were two behavioral variants (Experiment 3), as soon as one strategy became the majority by chance, new observers would more frequently witness that stimulus as predicting reward, and thus that option would be more strongly reinforced.

Exactly what is "social" in social learning is a multi-faceted question. Animals may have sensory and attentional systems tuned to social cues, which may then be moderated by individual experience (Leadbeater & Dawson, 2017). In Bridges et al., observer bees were likely drawn to conspecifics, but could also directly pair the colored tab with reward themselves through direct sampling. As such, it is not clear whether learning success was driven by bees observing demonstrators, or through them being more likely to gain rewards themselves via the puzzle-box already having been opened and rewards made available. These two non-exclusive possibilities could be teased apart by having "yoked" controls, where puzzle-boxes open (e.g., by hidden magnets), allowing observers to access rewards, but without demonstrators present. Previous work including this control (Loukola et al., 2017) found that using a magnet to create "ghost" movement of stimuli enhanced learning over no-demonstrator conditions, but not to the extent as having a demonstrator, indicating that both conspecific cues and other influences play a role in enhancing learning in the experimental treatments in Bridges et al.

In exploring the establishment of new, learned behaviors, Bridges et al. (along with other work using similar terminology, e.g., Loukola et al., 2017) highlight the novel behavior as "unnatural." On the face of it, solving the puzzle-box does indeed appear to be a "novel, nonnatural foraging behaviour." One of the (often endearing) perks of working with bumblebees is their aptitude for visiting novel types of "flowers": artificial flowers have been used in countless experiments since the time of Karl von Frisch and Charles Henry Turner. Honeybees and bumblebees may be particularly apt at visiting artificial flowers (lacking the scent, texture etc. of a real flower), because, as generalists, they visit a vast variety of floral species, which vary across a number of traits spanning modalities and morphologies, and requiring different handling strategies. From a human perspective, an artificial flower may appear more "natural" than solving a puzzle-box or rolling a ball (as in Loukola et al., 2017), yet in all cases, a bee encounters a stimulus (e.g., sees a color), performs a motor action (e.g., pushes with its body or scrabbles with its legs), and gains a sucrose reward. Each of these components are analogous to a natural foraging scenario. Thus, the cognitive mechanisms behind seemingly novel and complex behavior may be explained via the same associative mechanisms bees use when foraging on natural flowers. Creating a division between natural versus unnatural stimuli, and "behavioral innovations" versus natural foraging behavior, is therefore not clear-cut, and necessitates careful consideration from the animal's sensory and cognitive perspective.

Whether bumblebees establish persistent cultures in the wild is unanswered, yet many (including Darwin) have suggested that social learning may play a role in the context of nectar-robbing. In environments that have warm climates year-round, many bumblebee species are active throughout the winter, leading to the possibility of social information spread across different colonies, and even species. However, it is perhaps even more exciting if bumblebees do not socially learn and/or establish behavioral traditions in the wild, but can under laboratory settings, since it demonstrates the cognitive underpinnings necessary and sufficient for such behavior may be widespread and thus could readily be honed to a social context when favored by selection.

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