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Bumble bee string-pulling skill spreads between colonies under open diffusion conditions

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Socially transmitted behavioural traits can, if they persist in a group of animals over time, give rise to locally adapted phenotypes that can enhance survival. This capacity is widespread through the animal kingdom, and forms the foundation of cultural inheritance. While social learning is well documented among insects, and particularly in social insects such as bumble bees, the extent to which such behaviours can spread beyond initial kin groups and persist over time remains largely unknown. String pulling is a non-natural foraging behaviour where bees must manipulate a string to extract an out-of-reach artificial flower and collect a reward, and has previously been shown to spread via social learning. However, this was demonstrated only in highly controlled paired dyad settings, where interactions between bees were strictly limited. Here, we show that string pulling can spread both within and between bumble bee colonies, and persist over time, under previously untested open diffusion conditions. These are of greater ecological validity compared with classical paired dyad paradigms, and involve the seeding of a manually trained demonstrator into a group of naïve conspecifics. From this single point of origin, string-pulling behaviour spread rapidly within original, 'primary' colonies. Once the behaviour was established in the primary colonies, 'secondary' colonies were introduced, and string pulling was also acquired by these new foragers. Furthermore, string pulling was acquired through individual trial-and-error learning by a small number of bees in control colonies, which lacked trained demonstrators. These results confirm and build upon previous findings in bumble bees, and contribute to a growing body of evidence suggesting that social learning enables animals to establish local behavioural adaptations in the absence of the computational power provided by large brains.

In order to survive in any particular habitat, organisms must adapt to suit the specific demands and constraints of that habitat, from its climate to the availability of its resources, and to other species sharing it. This generally results in alterations to an organism's phenotype: its physical appearance, developmental processes or behaviour. While some traits are largely genetically constrained and shaped over multiple generations, and thus are limited in their ability to keep pace with increasingly rapid environmental change, others are more flexible and responsive to their environment. One such adaptive trait is behaviour, where behavioural plasticity provides faster, more flexible ways for animals to adapt (Snell-Rood, 2013). In particular, altering one's behaviour can allow the exploitation of novel resources that might appear in one's environment. In the United Kingdom, birds (most notably blue tits, *Cyanistes caeruleus*, and great tits, *Parus major*) learned to peck through foil milk bottle tops to access the cream (Fisher & Hinde, 1949). In Australia, sulphur-crested cockatoos, *Cacatua galerita*, discovered how to break into rubbish bins and overcame many human attempts to stop them (Klump et al., 2021, 2022).

At least in the first instance, novel behaviours such as these had to emerge through individual learning processes, such as trial-and-error. However, individual learning consumes time and energy, and can be risky. In contexts such as foraging on novel items or interacting with new species, making the wrong decision can be fatal (Laland, 2004). When a successful outcome of such individual learning is acquired by the innovator's conspecifics via social

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learning, though, it can result in the rapid spread of beneficial new behaviour throughout a population. When this persists over time, it essentially acts as a behavioural 'tradition' (Fragaszy & Perry, 2003) and can be considered a unit of culture. Often termed a 'second form of inheritance' (Whiten, 2017), and once thought wholly unique to humans, culture-like phenomena are increasingly understood to be prevalent throughout the animal kingdom. For example, chimpanzees, *Pan troglodytes*, from one location use stone tools to crack nuts while their neighbours do not (Boesch et al., 1994; Gunasekaram et al., 2024), and male humpback whales, *Megaptera novaeangliae*, have been found to change their songs to follow new trends (Garland et al., 2011). The majority of studies concerning culture in animals have focused on vertebrates with relatively large brains, as these, along with the 'complex' cognitive abilities they support, were deemed vital prerequisites (Boyd & Richerson, 1996). However, similar phenomena have since been demonstrated in a very different species: the bumble bee *Bombus terrestris* (Bridges et al., 2023). If opportunity arises, bumble bees too are capable of sustaining their own local variations in their behaviour: in this case, opening an artificial flower in the form of a puzzle box in one of two possible ways, with dynamics mirroring those previously observed in chimpanzees (Whiten et al., 2005), vervet monkeys, *Chlorocebus pygerythrus* (van de Waal et al., 2013) and great tits (Aplin et al., 2015).

Bombus terrestris is a primitively eusocial insect that lives in colonies of up to ca. 400 individuals (Goulson, 2010), and is an excellent model for social learning studies in the laboratory. These bumble bees readily learn novel, non-natural foraging behaviours such as pulling strings in exchange for rewards, either through incremental training by an experimenter or through social learning from their trained conspecifics (Alem et al., 2016). However, the spread of this behaviour was not tested under so-called 'open diffusion' conditions (Whiten & Mesoudi, 2008). Open diffusion paradigms involve the seeding of a trained individual into a larger group of animals, who are then all permitted to interact freely with the substrates necessary to perform the target behaviour with minimal interference from the experimenter. They are considered to be of greater ecological validity for group-living animals when compared with paired dyad paradigms, and better represent the spread of novel behaviour as a local adaptation in the group concerned. Thus, in the present study, we sought to build on our previous work on bumble bee social learning by monitoring the spread of string pulling under open diffusion conditions. In particular, we investigated whether the spread of string pulling would be limited to a single colony, or could spread beyond these limits to new, naïve colonies after being established in just one. Demonstrating between-colony transmission would confirm that cultural traits can move beyond the confines of a single, genetically related group in bumble bees, suggesting that these behaviours are unlikely to represent isolated phenomena and can spread beyond localized groups. Furthermore, our finding that some bumble bees were able to acquire string pulling in the absence of a trained demonstrator mirrored previous results with our puzzle-box paradigm (Bridges et al., 2023), and confirmed the impressive capacity for behavioural flexibility in bumble bees. Taken together, our results highlight and characterize a possible route through which novel foraging adaptations could naturally emerge and become established among bumble bee populations in the wild.

METHODS

Animal Model

Commercially raised *B. terrestris audax* colonies ($N = 9$) were supplied by Agralan, Ltd. (Swindon, U.K., https://www.agralan.co.uk). Upon arrival, each colony was transferred to bipartite wooden nestboxes (40.0 × 28.0 cm and 11.0 cm high), consisting of a covered nest chamber and a vestibule. During transfer, all individuals were marked with uniquely numbered opalith tags, to enable accurate identification and tracking of individual behaviour throughout the experiment. This was achieved by trapping each bee in a specially designed cage, lightly pressing it against a mesh ceiling with a sponge and fixing the tag to the thorax with superglue. Bees that eclosed during the experiments were also tagged once they attempted to leave the nest. During the experiment, bees were fed with commercially available pollen every 2 days and sucrose solution (20% w/w) every day, and were maintained at standardized temperature of 23 °C.

With bumble bees, and within our open diffusion experimental design, it is very difficult to provide a true measure of the potential pool of foragers that will be available in any one colony at any one time. The number of bees in a colony naturally fluctuates as new bees emerge and old bees die, and the number and identity of bees actively foraging for the colony rather than performing other, within-colony tasks is also subject to constant change. Thus, we aimed to select colonies for the experiment that were roughly the same size and age, with none being noticeably smaller or larger than another. Colonies C1, C2 and C3 were seeded with trained demonstrators and used as primary experimental colonies during the first phase of the experiment (phase I), while colonies CC1, CC2 and CC3 served as controls. Colonies SC1, SC2 and SC3 were used as secondary colonies and introduced to the primary colonies during phase II of the experiment.

Experimental Set-Up and Artificial Flower Design

Each nestbox was connected to the experimental flight arena (120.0 × 100.0 cm and 37.0 cm high; Fig. 1a) via a transparent Plexiglas corridor (25.0 × 3.5 cm and 3.5 cm high), which had plastic sliding stoppers inserted into 1.0 mm wide gaps along its length. These controlled which bees were able to enter the flight arena. The flight arena itself was covered with a transparent Plexiglas lid that prevented bees from escaping and permitted close observation, and was bipartite: a removable central cardboard wall created two separate experimental arenas. This allowed simultaneous experiments to be conducted.

The artificial flowers (Fig. 1a, inset) consisted of yellow polyurethane discs (diameter 3.0 cm), with a central sucrose reservoir made from an Eppendorf cap (diameter 0.5 cm). A 5.0 cm length of cotton string was hot-glued to the edge of each flower. These flowers were placed under a transparent sheet of Plexiglas (6.0 × 120.0 cm), so that they could be observed at all times by the experimental bees. This Plexiglas sheet was positioned 0.6 cm above the arena floor to prevent bees squeezing beneath it and reaching the reward without string pulling. A 2.0 cm tall hole was cut into the side of the box to allow the flowers to be removed, refilled and replaced from the outside, without needing to remove the flight arena lid, and the Plexiglas sheet over the flowers was angled upwards so that it covered this gap.

Experimental Protocol

Following initial acclimatization to the arena and artificial flowers via group pretraining, and the selection and training of a demonstrator, the cultural transmission experiment was divided into two main phases as follows. Phase I involved the introduction of a trained demonstrator into a colony of naïve foragers (the 'primary population'), allowing us to observe the spread of the string-pulling behaviour through social learning and compare it to control colonies with no demonstrator. In Phase II, a secondary colony of

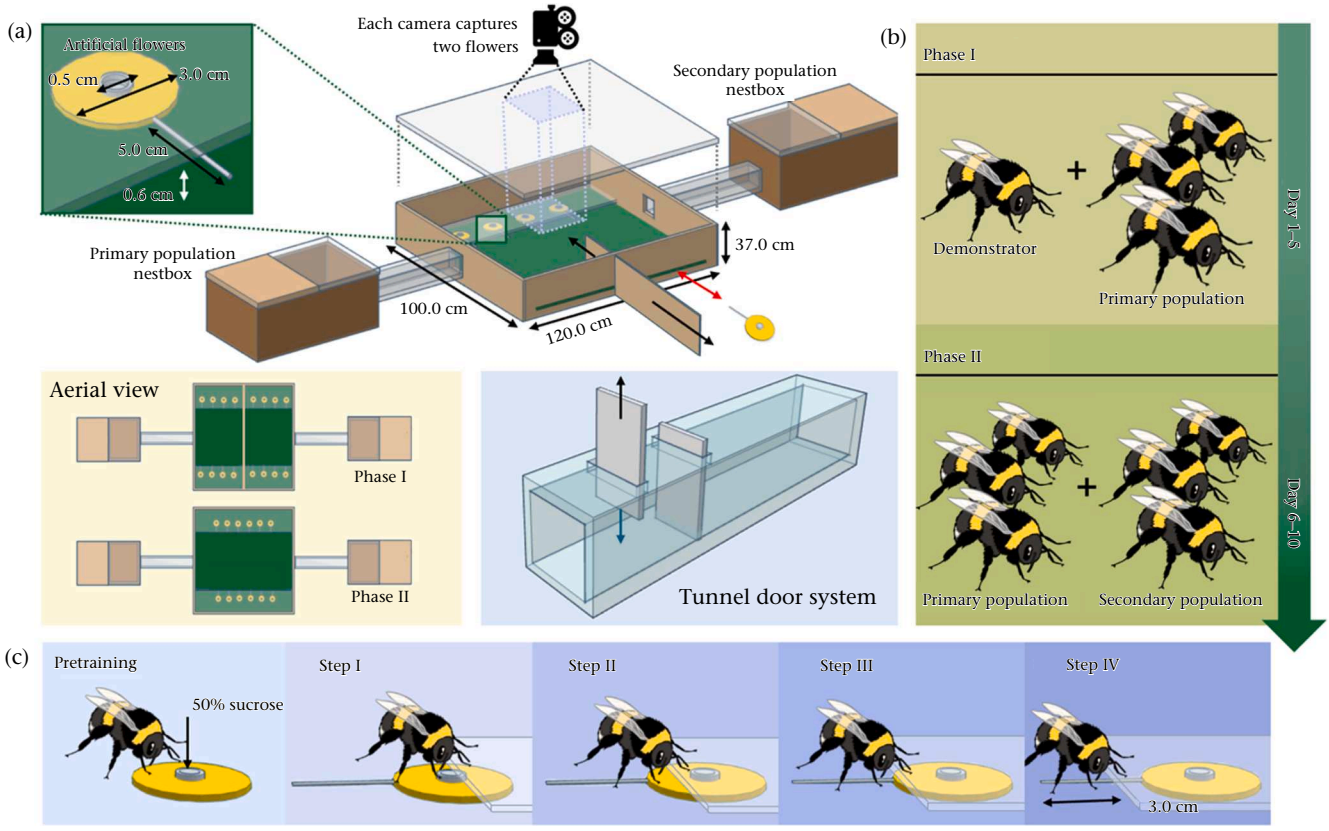

Figure 1. Experimental set-up and protocols. (a) Experimental set-up. The experimental arena was made bipartite by a removable divider, allowing for the connection of multiple colonies and the running of simultaneous experiments. Nestboxes were attached to the arena via acrylic tunnels, and a sliding door system (see inset) was used to control access to the arena. Either $N = 8$ or $N = 12$ artificial flowers were presented to the bees during phase I and II experiments, respectively, and could be removed from the arena by the experimenters through a small gap cut into the sides of the box. Cameras were positioned on top of the clear arena lid, and each field of view captured two of the artificial flowers. (b) Schematic of experimental phases. Phase I involved the training of a demonstrator by experimenters, and then tracking the spread of this behaviour throughout the demonstrator's home colony (the 'primary population') under open diffusion conditions for 5 days. Control colonies were exposed to the artificial flowers for the same length of time, but no trained demonstrator was added. Phase II involved the introduction of another colony (the 'secondary population'), which was allowed to forage alongside the primary colony for a further 5 days. (c) Stepwise demonstrator training protocol, as described in Alem et al. (2016). All bees used in the experimental and control open diffusion experiments underwent the pretraining phase, to familiarize them with foraging on the yellow artificial flowers. Once an individual had been selected for demonstrator training, it proceeded through steps I–IV in isolation from other bees. In step I, 50% of the flower was positioned beneath the Plexiglas sheet, with the sucrose reservoir partially accessible. In step II, 75% of the flower was positioned beneath the Plexiglas, forcing bees to physically move the flower to obtain the reward. In step III, the flower was positioned entirely beneath the Plexiglas, and in step IV, it was moved even further back, with ca. 3.0 cm of the string being the only protruding element.

naïve bees (the 'secondary population') was introduced to forage alongside the primary population, testing the transmission of learned behaviour across colony boundaries (Fig. 1b). All experiments were conducted under standardized artificial lights (12:12 h light:dark cycle; high-frequency fluorescent lighting provided by TMS 24F lamps with HF–B 236 TLD 4.3 kHz ballasts: Koninklijke Philips NV, Amsterdam, the Netherlands, https://philips.com/global; fitted with Activa daylight fluorescent tubes: OSRAM Licht AG, Munich, Germany, https://www.osram.com).

Initial acclimatization and group pretraining

This process was conducted for each colony, to ensure all bees were familiarized with the arena and needing to forage there. First, for 24 h, all bees were permitted to freely enter and forage from a central gravity feeder (containing 20% w/w sucrose solution). Following this, eight artificial flowers without strings attached were randomly positioned throughout the arena, each containing 50 μL of 50% w/w sucrose solution. Bees were permitted to forage on these flowers for a further 8 h. This not only allowed bees to associate the yellow flowers with reward, but also enabled the identification of suitable candidates for demonstrator training. Only those individuals that made repeated, consecutive foraging trips throughout this 8 h period were selected to undergo demonstrator training.

Stepwise demonstrator training protocol

One individual per phase I experimental colony was selected to undergo demonstrator training, with all other bees restricted to the nestbox to prevent familiarization with the task. Training was performed using the protocol previously described for the original dyadic transmission chain experiments (Alem et al., 2016). In brief, the selected bee was presented with artificial flowers ($N = 4$), each attached to a string with 50 μL of 50% w/w sucrose in the reservoir. However, in subsequent foraging sessions, these flowers were gradually positioned further underneath the clear Plexiglas sheet (Fig. 1c). Steps I–II do not require any manipulation of the flower itself, with the reward being accessible through the extension of the proboscis through the gap beneath the Plexiglas sheet: that is, the flower is not necessarily manipulated towards the individual and can remain in its initial position. However, the bees learn to reach beneath the gap to obtain the reward. By step III, the flower does need to be brought towards the bee for the reward to be extracted, but this can be achieved by moving the foam disc. In step IV, the final step, this is no longer possible: the artificial flower

is positioned ca. 2.0 cm under the Plexiglas, meaning bees must manipulate the string with either their legs or mandibles to pull the flower out from underneath. For steps I–III, each bee was given five foraging sessions, each lasting 5 min. If the bee failed to successfully extract a reward within 5 min, the artificial flowers were moved back to the previous step in the training sequence, requiring the bee to repeat that step in its entirety (e.g. they would be moved back to step II if the bee had failed in step III, and need to complete five more 5 min step II foraging sessions before proceeding to step III again). This was done to ensure that the bee could obtain a reward in each session, which maintained their motivation to continue training. After obtaining the reward in all five step III trials, the bees moved on to a final step IV, where the reward could only be accessed by directly manipulating the string. Once a bee obtained the reward through string pulling for the first time in step IV, it received 10 more 5 min trials with 10 artificial flowers. If the bee successfully demonstrated string pulling in all 10 tests, it was considered fully trained and became a demonstrator. For examples of string-pulling behaviour, see Videos 1–3 in the Supplementary Material.

Phase I

To investigate the spread of string pulling as a cultural tradition, we adopted an 'open-diffusion' paradigm (Whiten & Mesoudi, 2008). Here, all individuals within a population are allowed to freely interact with their conspecifics and the necessary materials to perform a target behaviour, without encouragement or hindrance from experimenters. Similar open diffusion experiments have been successfully conducted in bumble bees previously, although with a different task (Bridges et al., 2023). Control colonies underwent the same procedures as the experimental colonies, but lacked trained demonstrators.

After a demonstrator was successfully trained (one per experimental colony), phase I of the experiment began. During phase I, open diffusion experiments were conducted every day for 5 consecutive days. With a single 3 h experimental session conducted per day, bees had a total of 15 h exposure to the string-pulling task during this phase. Before each experimental session, bees were given a 1 h 'refreshment' pretraining period, where they were allowed to forage on stringless, randomly placed, readily accessible artificial flowers ($N = 8$, each containing 50 μL of 50% w/w sucrose solution). This ensured that the association between the artificial flowers and the reward was maintained. As bumble bees are central place foragers and typically continue to forage for the colony even when individually sated, the pretraining was unlikely to have a negative influence on individual motivation. Rather, this pretraining served to raise foraging motivation before the experimental session: bumble bees constantly monitor the content of their honey pots (Dornhaus & Chittka, 2005), and an influx of relatively high-quality sucrose (50% versus the maintenance 20% sucrose diet) may have encouraged more bees to emerge from the colony and attempt to forage themselves.

The experimental session began immediately after pretraining. Here, bees were presented with $N = 8$ artificial flowers positioned underneath the Plexiglas sheet as in step IV of demonstrator training, with only the strings accessible, for a period of 3 h. Flowers were evenly spaced (15.0 cm apart), with four on each side of the arena: this limited undesirable mass aggregations of foraging individuals in any one spot. Flowers were continuously refilled when depleted, using metal wire hooks to pull them through the gap in the side of the arena (Fig. 1a). After the experimental period was over, the artificial flowers were removed, all bees were returned to the nestbox and the arena interior, artificial flowers and strings were cleaned with 70% ethanol. This was done to reduce any possible confounding influence from olfactory cues that might have been left behind ('residual traces'; see Sherry & Galef, 1984).

Phase II

The phase II open diffusion experiments occurred immediately after phase I and followed the same protocol, but the divider was removed from the flight arena to allow two colonies (one phase I experimental colony and one naïve secondary colony) to forage together on $N = 12$ artificial flowers, each containing 50 μL of 50% w/w sucrose solution (Fig. 1a). Phase II continued for 5 days, with a single 3 h experimental session per day. This resulted in a total of 15 h exposure to the string-pulling task during phase II, and 30 h when combined with phase I. After each phase II experimental session ended, bees were sorted and returned to their original nestboxes.

Video Analysis

All observations were recorded using Handycam HDR-CX 190E cameras (Sony, Tokyo, Japan, https://www.sony.com) positioned on the top of the transparent flight arena lid. A total of four cameras were used per diffusion experiment, with each field of view capturing two artificial flowers (Fig. 1a). Thus, phase I elicited 4×15 h of video footage for each experimental colony (180 h total) and 4×15 h of video of each control colony (180 h total); with a further 4×15 h of video being obtained during each phase II experiment (180 h total). Thus, 540 h of video footage in total was obtained for analysis.

We used BORIS software (Friard & Gamba, 2016) to record each instance where flowers were extracted via string pulling as a point event. As each bee was tagged, we were able to assign each string-pulling event to the ID of the exact individual who performed it, building a picture of how each bee interacted with the string-pulling task over time. For an extraction to be assigned to a bee as a 'string-pulling event', the bee had to either fully extract the flower by clearly manipulating the string, or initiate/finalize the extraction by pulling the string for at least 50% of the length required to obtain the reward while surrounded by conspecifics. If the extraction could not be clearly attributed to an individual bee (e.g. multiple bees manipulated the string simultaneously, or the flower was extracted by squeezing under the table rather than directly manipulating the string with mandibles and legs; see Video S4 in the Supplementary Material for an example), this was coded as a 'nonpulling extraction' and was assigned to no particular bee.

The criterion used to determine whether an individual had learned was the same as used in our previous work (Bridges et al., 2023): once a bee had performed string pulling twice, it was considered to have learned the behaviour.

O.P. acted as first scorer for the videos, with A.D.B. acting as second scorer on a randomly selected subset of 18 videos (representing 54 h of the total 540 h of video, i.e. 10% of the overall footage), which were drawn from all colonies and conditions. Neither scorer was hypothesis-naïve, but A.D.B. was blind to the colony, condition and experimental day that each video represented. There was 95.31% agreement between the scorers across this subset of videos.

Statistical Analyses

Data were plotted and analysed using R version 3.2.2 (R Core Team, 2015). We conducted generalized linear mixed models (GLMMs) with model selection based on AIC comparisons. Specifically, we considered the model with the lowest AIC score the best model; that is, the model that provides a satisfactory explanation of the variation in the data (Johnson & Omland, 2004).

Following accepted convention, models with an AIC difference of less than two units were considered not significantly better than the model it was being compared to (Burnham & Anderson, 2004); thus the simpler model was selected. Model diagnostics were performed using the DHARMa package (Hartig, 2016) to assess and validate model fit. All final model summaries were reported with ANOVA using the car package (Fox et al., 2001). Post hoc tests and pairwise comparisons were performed using the emmeans package (Lenth, 2017) and adjusted using Bonferroni corrections when needed.

To analyse learning across days (both phase I and phase II; Figs. 2a,b, 3a,b), we applied Poisson or negative binomial generalized linear mixed models (GLMMs) depending on model fit. The response variables were the cumulative number of learners or the total number of string-pulling events, with fixed effects for observation day, demonstrator presence (experimental or control for phase I) and colony type (primary or secondary for phase II). Random effects were included for the individual colonies tested.

For the learning proficiency analysis (Figs. 2c and 3c), we performed a gamma GLMM with a log link. A 'proficiency index' was calculated as previously described in Bridges et al. (2023) and defined as the total number of pulling occurrences divided by the number of days spent as a learner (which was inclusive of the day that the learning criterion was met). This index therefore reflected how consistently individuals used string pulling after meeting the learning criterion. When comparing proficiency between experimental and control colonies in phase I, the models included fixed effects for the presence of a demonstrator, with colony as a random factor. For comparisons of learning proficiency between primary and secondary colonies, fixed effects of colony type (primary phase I, primary phase II and secondary phase II) were included, with colony as a random factor.

The relative contribution of each individual across the phase I and II diffusion experiments (calculated as the ratio of an individual's total number of string-pulling occurrences on a given day to the total number of string-pulling occurrences by the entire experimental population on that day) was analysed using beta family GLMMs. The number of 'pullers' (total number of bees demonstrating string pulling on a given day), observation day, colony type (primary or secondary) and learning timing (three level factor, with 'early learners' meeting criterion on days 1–3, 'mid learners' on days 4–6 and 'late learners' on days 7–10) were included as fixed factors. To account for individual variability, bee ID was included as a random factor. Significant interactions were further explored using post hoc pairwise comparisons of the slopes. $P < 0.05$ was considered to indicate a statistically significant difference.

Ethical Note

No ethical review or approval from a regulatory body was required for this experiment on bumble bees. However, all experiments were conducted by researchers trained in the proper handling and maintenance of bumble bees, and every effort was taken to minimize stress to the subjects. Direct handling was kept to a minimum, only occurring during individual tagging. Bumble

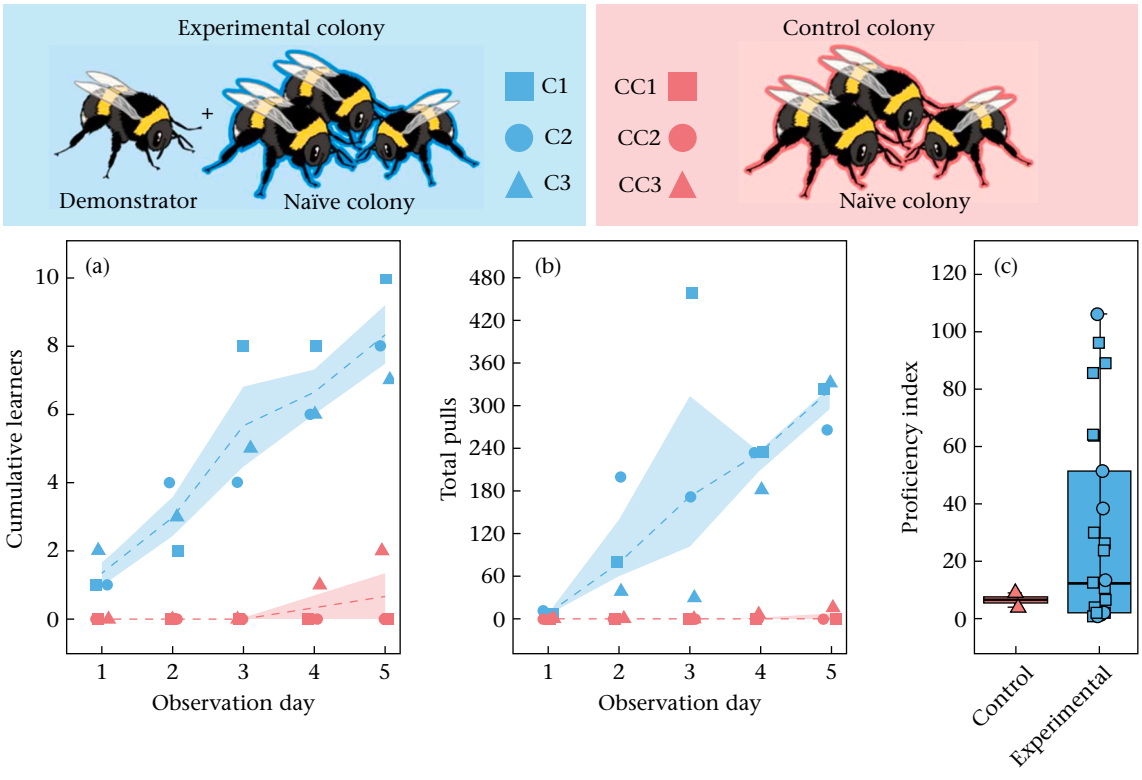

Figure 2. Social learning drives the acquisition and proficiency of the string-pulling technique in bumblebees. (a) New learners steadily accumulated in the experimental colonies (blue), while control colonies (red) showed minimal learning. (b) The number of string-pulling events recorded each day also increased in the experimental colonies as the diffusion progressed. The dashed lines depict the average number of learners within the group (experimental or control) across days, while shaded areas show the interquartile range for experimental (blue) and control (red) colonies. (c) The proficiency index, calculated as the total pulling occurrences/number of days spent as a learner, compares individual performance between the groups. Although not statistically significant, there was a trend where learners in experimental colonies (blue, $N = 25$) exhibited greater overall proficiency in string-pulling behaviour compared to those in control colonies (red, $N = 2$). Individual-level data underlying this figure are presented in Fig. S1–S4, in the Supplementary Material. The box represents the Interquartile Range (IQR), with the internal horizontal line showing the group median; the whiskers extend to the data points closest to, but not exceeding, 1.5 times the IQR from the box.

bees were never made to take part in experiments on the same day that they had been marked: although this process was noninvasive, they were allowed to recover and acclimate in their nestbox without further interference. In cases where bees were tagged during the course of an ongoing open diffusion experiment, they were permitted to leave the nest and participate if they so chose but were not 'encouraged' to do so. Bees were allowed to move freely in the flight arena during the diffusion experiments, and were never physically forced to participate in the experiments. Nestbox vestibules were regularly cleaned of debris and waste, and colonies had free access to food outside the daily experimental period. As these were commercially bred bumble bee colonies, it was not possible for them to be released to the wild after use in our experiments: thus, colonies were euthanized by freezing when they showed signs of ageing and collapse, in accordance with standard practice. We also aimed to use the minimum number of colonies possible for this experiment.

RESULTS

Social Learning Drives String Pulling Acquisition and Proficiency

By the end of the phase I open diffusion experiment, bees from all three experimental colonies had met the learning criterion and acquired string pulling (colony C1, $N = 10$, C2, $N = 8$ and C3, $N = 7$; Fig. 2a, Table 1). Notably, while no learners emerged in the control colonies CC1 or CC2, some bees ($N = 2$) from control colony CC3 did learn string pulling. Despite having no trained demonstrator to model, bee g21 met the learning criterion on day 4, followed by bee o94 on day 5 (Fig. 2a, Table S4 in the Supplementary Material). However, these learners were fewer in number than those from the experimental colonies ($N = 2$ across three control colonies versus $N = 25$ across three experimental colonies), and both of them first met the learning criterion later on in the experiment (on days 4 and 5, compared with as early as day 1 in the experimental colonies; Fig. 2a, Table S1–S4).

To assess whether the number of new learners varied significantly across days between the experimental and control colonies, we fitted a Poisson generalized linear mixed-effects model. The best-fitting model included observation day and the presence of a demonstrator as main effects, but no interaction between these (see Table S6 for model selection details). As anticipated, both factors significantly influenced the cumulative number of naïve bees learning string pulling over the 5 days (Fig. 2a). Specifically, the number of learners ($N = 25$ across three experimental colonies) significantly increased as the days of observation progressed ($\chi^2_1 = 20.20$, $P < 0.0001$) and in the presence of a demonstrator ($\chi^2_1 = 29.89$, $P < 0.0001$; Table S6), underscoring the importance of both temporal dynamics and social learning in the acquisition of the behaviour.

Next, we investigated whether the number of string-pulling instances by learners changed over the course of the diffusion experiment, and whether this change differed between control and experimental colonies: in short, did learners become more proficient at string pulling with time, and did their proficiency increase more rapidly with a demonstrator present? The best-fitting model included both observation day and the presence of a demonstrator as main effects, with no interaction between these (see Table S7 for model selection details). As with the total number of learners, the number of pulling events steadily increased across the observation days in both groups ($N_{exp} = 2675$ string pulling events by $N = 25$ learners, and $N_{ctrl} = 23$ string pulling events by $N = 2$ learners; $\chi^2_1 = 28.08$, $P < 0.0001$; Table S7). However, the presence of a demonstrator significantly increased the overall number of pulling instances compared with the control ($\chi^2_1 = 33.26$, $P < 0.0001$; Fig. 2b, Table S7). This may have occurred because the presence of the demonstrator facilitated interest in the flowers on the part of observers: notably, there was also a significant increase in flower extractions without clear use of the string-pulling technique in the experimental colonies compared with the control colonies ($N_{exp} = 1053$ and $N_{ctrl} = 94$ nonpulling extractions; $\chi^2_1 = 42.91$, $P < 0.0001$; Fig. S5, Table S5). Once the first bee learned to string-pull in a control it did technically become a demonstrator for those that followed, but the number of string-pulling events performed by this first learner was not closely comparable to the number performed by our trained demonstrators ($N = 7$ instances on day 4 and $N = 11$ on day 5, compared with $N = 56$, 121 or 145 string-pulling events produced by trained demonstrators on phase I day 1 alone; Table S1–S4). This may have been the reason why fewer bees learned under control conditions.

As described previously (Bridges et al., 2023), since different learners acquired string pulling on different days, to compare their proficiency we used an index: the total pulling occurrences divided by the number of days spent as a learner, allowing us to compare how consistently individuals used string pulling after meeting the learning criterion. Interestingly, there was no significant difference in terms of proficiency between the experimental ($N = 25$) and control ($N = 2$) learners ($\chi^2_1 = 2.72$, $P = 0.09$; Table S8). The lack of significance here may be due to the small sample size for the control learners ($N = 2$, with a median proficiency index of 6.5, IQR 5.25–7.75; Fig. 2c). In contrast, the experimental group ($N = 25$) exhibited substantial variation in proficiency levels, with a median proficiency index of 12.5 (IQR 2–51.5; Fig. 2c). While the highest recorded proficiency index was 106, a notable portion of experimental learners (9 out of 25) had a proficiency index <4, which was lower than the smallest value observed in the control group. The control learners both remained at the lower end of this scale, with proficiency indices of 4 and 9.

String-Pulling Spreads Between Unrelated Colonies

After confirming that string-pulling acquisition and proficiency within a single colony was highly dependent on the presence of a demonstrator in our open diffusion paradigm, we next examined whether this learned behaviour could continue to spread beyond this initial colony. Specifically, we sought to determine whether string pulling could be transmitted to secondary colonies of genetically unrelated naïve bees, continuing the learning process across colony boundaries. At the end of phase I, 10, 8 and 7 naïve bees in the experimental colonies C1, C2 and C3, respectively, had met the learning criterion. In phase II, we continued the open diffusion experiments by introducing a new secondary colony to each primary colony, and recorded the number of new bees that acquired string pulling in both colonies.

As before, we assessed whether the number of new learners continued to increase over phase II, and whether this rate of increase differed between primary colonies (those exposed to 5 days of open diffusion previously, during phase I) and secondary colonies (newly introduced and naïve to the string-pulling technique at the start of phase II). Indeed, bees from all three secondary colonies learned to string pull during phase II (SC1, $N = 4$, SC2, $N = 7$ and SC3, $N = 6$; Fig. 3a). When controlling for the random effect of colony ID, the best-fitting model included fixed effects for observation day and colony type (primary or secondary), along with their interaction (see Table S9 for model selection details). Our analysis revealed a significant increase in the number of new learners in both the primary ($N = 7$) and secondary colonies ($N = 17$) across the 5 days of phase II ($F_4 = 26.98$, $P < 0.0001$; Table S9). While the fixed effect of colony type was not statistically

significant ($F_4 = 1.59$, $P = 0.276$), the significant interaction between colony type and observation day ($F_4 = 10.88$, $P = 0.0002$) indicated that learning rates varied between primary and secondary colonies over time. Post hoc analyses showed no significant differences in the number of new learners between the two colony types during days 1–3 (Fig. 3a, Table S9). However, by day 4, a higher number of new learners emerged from the secondary colonies, with the difference becoming statistically significant on day 5 (estimate ± SE = −3.33 ± 1.04, $t_{5.71} = -3.19$, $P = 0.020$; Table S10). This pattern suggests that secondary colonies displayed a faster learning rate during the later days of phase II.

Next, we assessed the number of string-pulling occurrences, using the total number of string-pulling events by learners as the response variable (see Table S11 for model selection details). This analysis revealed that pulling events by learners also increased significantly with observation day ($\chi^2_1 = 37.28$, $P < 0.0001$), with learners from secondary colonies performing string pulling significantly more often during phase II ($N = 1252$ string pulling events by $N = 17$ learners) than those from the primary colonies who learned during phase II ($N = 163$ pulling events by $N = 7$ learners; $\chi^2_1 = 5.01$, $P = 0.025$; Fig. 3b, Table S11). Despite bees pulling more frequently, however, post hoc analyses showed that by the end of phase II, the proficiency indexes of learners from secondary colonies ($N = 17$, median = 7.9, IQR 6.0) were not significantly different from those in primary colonies that learned during either phase II ($N = 7$, median = 2.8, IQR 1.4; estimate ± SE = −0.66 ± 0.76, $z = -0.88$, $P = 0.656$) or phase I ($N = 25$, median = 12.5, IQR 49.5; estimate ± SE = 0.81 ± 0.71, $z = 1.15$, $P = 0.483$; Fig. 3c, S13). Interestingly, there was a significant decrease in proficiency in learners from primary colonies in phase II compared to learners from primary colonies in phase I (estimate ± SE = 1.48 ± 0.61, $z = 2.43$, $P = 0.040$; Table S13). This decline may represent a reduction in the opportunity for these phase II learners to demonstrate string pulling, due to increased competition for the flowers during later stages of the experiment. In our set-up, a limited number of flowers were available for pulling at any one time, and the number of learners and number of string-pulling events were both significantly positively correlated with the number of nonpulling extractions (learners versus nonpulling extractions, Spearman $\rho_{28} = 0.48$, $P = 0.007$; string-pulling events versus nonpulling extractions, Spearman $\rho_{28} = 0.57$, $P = 0.001$; Fig. S5). Increased activity around the flowers could have limited the opportunities for newer learners to practise, consolidate or display their string-pulling behaviour.

Impact of the Number of Knowledgeable Bees on String-Pulling Acquisition by New Bees

The main difference between the conditions naïve bees were exposed to in phases I and II was the number of knowledgeable

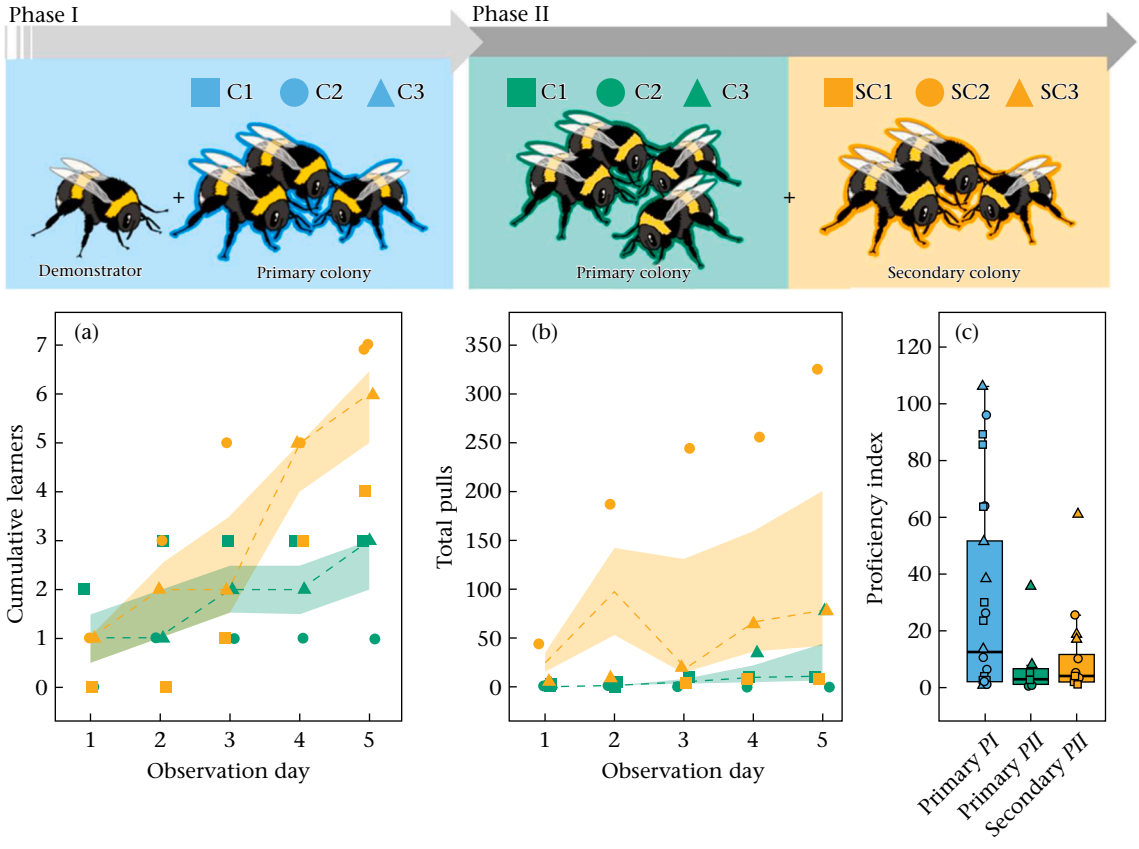

Figure 3. Social learning facilitates the spread of string-pulling behaviour across unrelated colonies. (a) New learners continued to accumulate from both the primary (green) and secondary (yellow) colonies during phase II, with a faster rate of learning observed in the secondary colonies from day 3 onwards. (b) The number of pulling events by these new learners, who met criterion during phase II, increased more rapidly among learners from the secondary colonies compared with those from the primary colonies. The dashed lines depict the group's average number of learners or pulling events across observation days, with shaded areas showing the interquartile range for primary (green) and secondary (yellow) colonies. (c) The proficiency index, calculated as the total pulling occurrences/number of days spent as a learner, compares individual performance across three groups: primary colonies in phase I (blue), primary colonies in phase II (green) and secondary colonies in phase II (yellow). Individual-level data underlying this figure are presented in Fig. S1–S3 in the Supplementary Material. The box represents the Interquartile Range (IQR), with the internal horizontal line showing the group median; the whiskers extend to the data points closest to, but not exceeding, 1.5 times the IQR from the box.

Table 1
Summary of colony-level data for phases I and II

Colony ID	Primary experimental colonies				Secondary experimental colonies				Control colonies			
	C1	C2	C3	All	SC1	SC2	SC3	All	CC1	CC2	CC3	All
Total learners[a]	13	9	10	32	4	7	6	17	0	0	2	2
In phase I	10	8	7	25	–	–	–	–	0	0	2	2
In phase II	3	1	3	7	4	7	6	17	–	–	–	–
Total pulls by learners[b]	2546	2409	2026	6981	19	1056	177	1252	0	0	22	22
In phase I	1102	884	585	2571	–	–	–	–	0	0	22	22
In phase II, by:									–	–	–	–
All learners	1444	1518	1441	4403	19	1056	177	1252	–	–	–	–
Phase I learners	1406	1515	1319	4240	–	–	–	–	–	–	–	–
Phase II learners	38	3	122	163	19	1056	177	1252	–	–	–	–
Average learner proficiency index (IQR)[c]												
Phase I learners	13.8 (52.9)	11.5 (30.5)	13.3 (43.3)	12.5 (49.5)	–	–	–	–	–	–	6.5 (2.5)	6.5 (2.5)
Phase II learners	1.3 (1.2)	0.3	5.1 (6.3)	2.8 (1.4)	0.6 (0.5)	16.1 (14.4)	3.2 (2.3)	7.9 (6.0)	–	–	–	–

	Experimental groups				Control colonies			
	C1+SC1	C2+SC2	C3+SC3	All	CC1	CC2	CC3	All
Total nonpulling extractions[d]	832	1690	689	3211	9	9	76	94
In phase I	334	413	274	1021	9	9	76	94
In phase II	689	274	415	1378	–	–	–	–

The raw, individual-level data underlying this table are presented in the Supplementary Material, in Table S1–S3 for the paired primary and secondary colonies C1 and SC1, C2 and SC2 and C3 and SC3, Table S4 for the control colonies CC1–CC3 and Table S5 for the non-pulling extractions.

[a] 'Learners' are untrained observer bees that met the learning criterion during the experiment: performing string-pulling behaviour twice.

[b] 'Pulls' refers to the incidence of string pulling: defined as any instance where an individual fully extracted the flower by manipulating the string or, if surrounded by conspecifics, contributed to the extraction by manipulating the string for at least 50 % of the required length to obtain the reward.

[c] The learner proficiency index, presented with the interquartile range in parentheses, was calculated for each individual by dividing its total number of pulls by the number of days it had spent active as a learner during the experiment (inclusive of the day on which it met the learning criterion). The phase I learners score refers to the proficiency of learners that met criterion in phase I, during phase I. The phase II learners score refers to the proficiency of learners that met criterion in phase II, during phase II.

[d] 'Nonpulling extractions' refer to incidences where flowers were extracted without string-pulling behaviour, or where the extraction of the reward could not be clearly attributed to string pulling by a single bee.

bees present at the start. In phase I, the diffusion process began with the introduction of a single trained demonstrator. However, phase II began with multiple knowledgeable foragers present from the start. To investigate the impact of this on the diffusion of string pulling, we directly compared learner accumulation and string-pulling performance between primary colonies during the 5 days of phase I and secondary colonies during the 5 days of phase II.

The best-fitting model comparing the number of cumulative learners between these groups included observation day and colony type (primary versus secondary), without interaction (Table S14). As before, observation day was a highly significant predictor of learner number, with more learners having emerged by later experimental days ($\chi^2_1 = 32.23$, $P < 0.0001$). Colony type, however, was also highly significant ($\chi^2_1 = 7.34$, $P = 0.007$), indicating that the difference in the number of learners between primary phase I and secondary phase II remained constant across days.

For the number of pulling events, the best-fitting model included observation day, colony type and their interaction (Supplementary Table S15). In both colony types, there was a significant increase in pulling events recorded over the diffusion days ($\chi^2_4 = 530.91$, $P < 0.0001$). Colony type was not significant as a fixed factor; however, the significant interaction between colony type and observation day indicates that the effect of group is dependent on the day ($\chi^2_4 = 52.84$, $P < 0.0001$). Indeed, post hoc analysis revealed a trend in which primary phase I colonies consistently exhibited more pulling events compared to secondary phase II colonies (positive estimates for all days; see Table S16). While these differences were not significant at the beginning of diffusion (day 1: estimate ± SE = 0.09 ± 0.94, $z = 0.09$, $P = 0.925$; day 2: estimate ± SE = 1.35 ± 0.91, $z = 1.49$, $P = 0.135$), they became statistically significant by day 3 (estimate ± SE = 1.79 ± 0.90, $z = 1.98$, $P = 0.048$). On subsequent days, the differences approached significance (day 4: estimate ± SE = 1.57 ± 0.90, $z = 1.74$, $P = 0.082$; day 5: estimate ± SE = 1.70 ± 0.90, $z = 1.88$, $P = 0.06$) but did not reach statistical significance after Bonferroni adjustment. These results suggest that differences in pulling behaviour between colony types became more pronounced over time, particularly starting from observation day 3, with primary colonies generally showing a stronger tendency for more pulling events compared to secondary colonies.

Restricted Resources May Limit Observer Performance

The trends we observed between the primary phase I and secondary phase II colonies seem counterintuitive. If the presence of a demonstrator is key to the spread of string pulling, as seen when comparing experimental colonies to controls, then why would an increased availability of demonstrators be no better, or worse, than having just one? Thus, we investigated whether other factors might be influencing the spread of string pulling in our experimental set-up.

Many naïve bees ($N = 24$ overall, with $N = 7$ from primary colonies and $N = 17$ from secondary colonies) reached the learning criterion during phase II. As aforementioned, while there was no significant difference between the proficiency of learners from the primary and the secondary colonies, there was still a decline in the overall proficiency of learners from phase I to phase II (Fig. 3c). This difference was most notable among learners from the primary colonies, with a significant decline from phase I to II (estimate ± SE = 2.46 ± 0.62, $z = 3.96$, $P = 0.0002$; Fig. 3c, Table S13). One explanation might be that the bees from the primary colonies, who learned during phase I, might be less active due to, for example, age. However, this alone did not explain the downward trend among learners from the phase II secondary colonies compared with those from phase I primary colonies (Fig. 3c).

Another possible explanation is that, as the number of knowledgeable bees present in the flight arena increased, the limited availability of artificial flowers for string pulling (with a maximum

of 12 flowers available at any given time) resulted in reduced opportunities for new bees to pull strings and demonstrate their learning compared with at the start of the experiment. Indeed, as the diffusion progressed and more bees acquired the technique, the total number of pulling events increased (Figs. 2 and 3). To explore this further, we investigated how the number of pullers active on a given day (no. of pullers) influenced the relative contribution of each individual to the total number of pulling events on that day. Raster plots for each pair of primary and secondary colonies revealed that at the start of the diffusion experiments, when there were just a few learners, a subset of these tended to disproportionately contribute to the daily total of string-pulling events (Fig. 4). As more bees began to learn, and particularly following the introduction of the secondary colonies, a more even distribution of activity was observed. To understand which factors, if any, drove this shift in relative individual contribution, we investigated the effect of colony type (introduction: primary or secondary), observation day (day) and when each bee met the learning criterion (criterion met: $N = 17$ early learners, on days 1–3; $N = 13$ mid learners, on days 4–6; $N = 19$ late learners, on days 7–10). The best-fitting model, which controlled for individual variation as a random effect, included fixed effects for the number of pullers each day (no. of pullers), learning time (criterion met), colony type (introduction phase) and observation day (day), as well as an interaction between the number of pullers and observation day (see Table S17 for model selection details).

The analysis revealed that observation day did not have a significant effect on performance ($\chi^2_9 = 11.08$, $P = 0.270$), indicating that performance changes are not driven simply by experimental progression but are rather impacted by other factors. Specifically, colony type (introduction phase) significantly influenced performance ($\chi^2_1 = 5.48$, $P = 0.019$), with bees from primary colonies outperforming those from secondary colonies (estimate ± SE = 0.694 ± 0.296, $z = 2.34$, $P = 0.019$). Performance also varied significantly based on when a bee met the learning criterion ($\chi^2_2 = 13.39$, $P = 0.001$); post hoc paired comparisons revealed that early learners had significantly better overall performance than mid learners (estimate ± SE = 0.74 ± 0.28, $z = 2.67$, $P = 0.021$) and late learners (estimate ± SE = 1.59 ± 0.59, $z = 2.71$, $P = 0.019$). At the same time, mid learners and late learners did not differ (estimate ± SE = −0.85 ± 0.60, $z = -1.41$, $P = 0.335$).

The number of pullers on a given day (no. of pullers) did not directly influence performance, although it showed a marginally significant effect ($\chi^2_1 = 3.56$, $P = 0.059$). However, there was a significant interaction between the number of pullers and when bees met the learning criterion ($\chi^2_2 = 7.30$, $P = 0.026$). Indeed, post hoc analyses revealed that early learners showed a strong trend towards declining performance as the number of learners increased (estimate ± SE = −0.07 ± 0.04, $z = -1.89$, $P = 0.059$). In contrast, mid learners (estimate ± SE = 0.185 ± 0.145, $z = 1.27$, $P = 0.205$) and late learners (estimate ± SE = 0.03 ± 0.04, $z = 0.68$, $P = 0.496$) showed no change in performance as the number of learners increased.

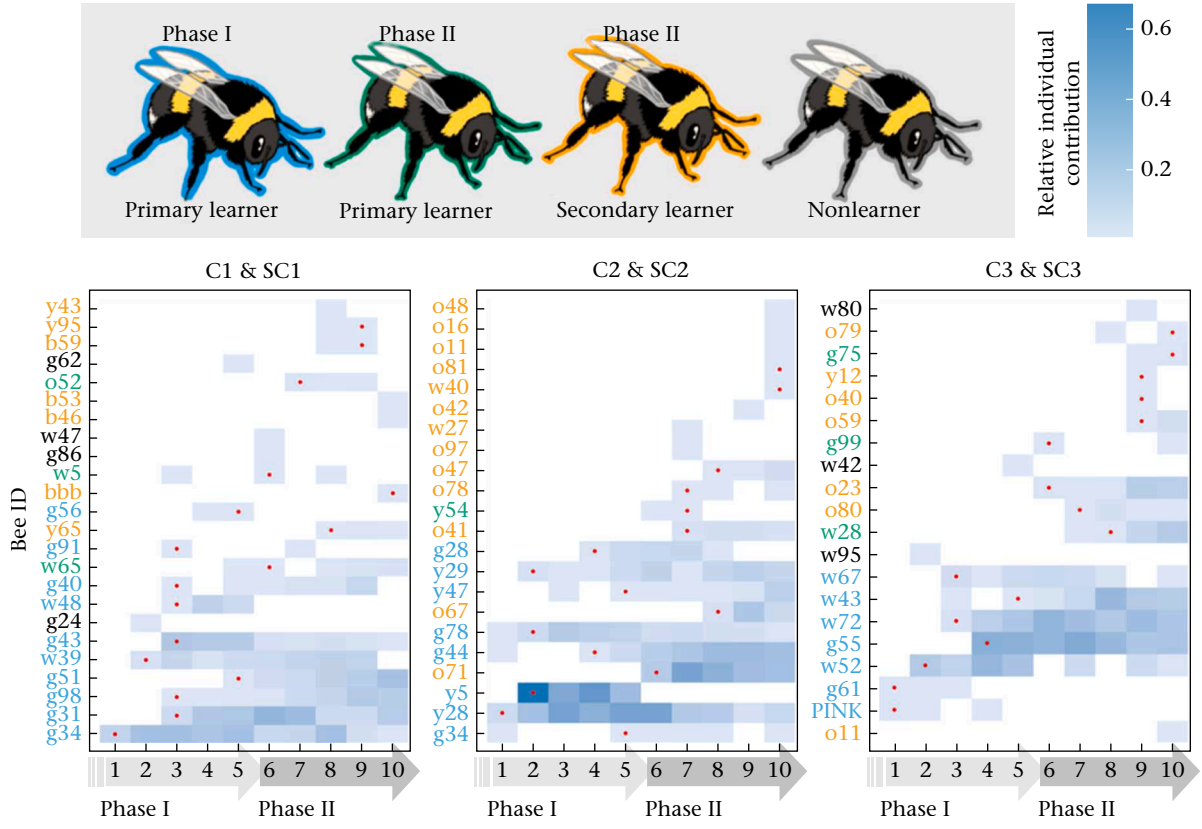

Figure 4. Restricted resources may limit the string-pulling performance of individuals under open diffusion conditions. The raster plots illustrate the relative individual contribution (total pulling occurrences for each bee adjusted for the total occurrences across all bees for a given day) across the observational days, for three experimental colonies during phase I and phase II: experimental colony 1 (primary colony C1 with a seeded demonstrator and secondary introduced naïve colony SC1), experimental colony 2 (primary colony C2 with a seeded demonstrator and secondary introduced naïve colony SC2) and experimental colony 3 (primary colony C3 with a seeded demonstrator and secondary introduced naïve colony SC3). Each row represents a single bee (with bee IDs from primary and secondary colonies shown in green and yellow, respectively). The level of shading indicates the proportion of total string-pulling events attributed to each bee on a given day, with darker shading representing a higher number of string-pulling events. Red dots indicate the day on which each bee met the learning criterion (performing string-pulling behaviour for the second time).

DISCUSSION

The results of the present study represent a clear confirmation of the potential for local behavioural adaptations to emerge among groups of bumble bees, if opportunity arises. The spread of string pulling from a single, experimenter-trained individual to multiple naïve observers, who then repeatedly performed the behaviour themselves, fulfils the definition of a behavioural tradition as used in animals (Fragaszy & Perry, 2003). A similar phenomenon was observed in previous work by our group (Bridges et al., 2023), using a different non-natural foraging paradigm: a puzzle box that had to be opened by rotating a lid. However, the present study builds on this further by demonstrating the spread of string pulling between unrelated colonies of bumble bees. Once string pulling was established in our primary experimental colonies, it readily spread through newly introduced secondary colonies. Comparable results have previously been found in captive chimpanzees: behavioural traditions established in one group later spread to others with a high degree of fidelity (Whiten et al., 2007). Here, groups of chimpanzees had visual access to neighbouring groups, and traditions spread serially across these groups. Our findings suggest that socially learned behaviour would also be able to spread beyond localized, related groups of bumble bees, should it ever arise in the field. When foraging outside the nest in the field, bumble bees are likely to have visual access to members of other groups. Estimates of the length of a typical foraging trip for *B. terrestris* vary among authors, with a 267.2 m average and 800 m maximum recorded by Wolf and Moritz (2008), and a 551 m average recorded by Redhead et al. (2016). Routine trips of 1.5 km have also been reported (Osborne et al., 2008). With such ranges, it is highly likely that members of other colonies would be routinely encountered by bumble bees, providing opportunity for foraging traditions to spread between groups.

Further analysis of our results provided additional insights about the spread of string pulling in our open diffusion paradigm. First, while the number of new learners from both primary and secondary colonies significantly increased during phase II, towards the end of this phase significantly more learners emerged from the secondary colonies. This may simply have been due to the pool of potential learners available within the primary colonies being exhausted by that point. Colonies of *B. terrestris* can grow to contain more than 200 workers (Sladen, 1912), but not all of these bees act as foragers at any one time. Although they do not show the strict age-dependent polyethism of honey bee workers, younger bumble bees tend to perform tasks within the nest and switch to foraging later on, although some individuals never make the switch (Goulson, 2010; Hoffer, 1882; Sladen, 1912). It is also possible that some of these foragers will never learn to string pull. Lack of motivation, neophobia or limitations in terms of cognitive capacity may reasonably be posited to prevent some individuals ever acquiring such behaviour. Any of these factors might limit the number of potential string pullers present in a single colony at any one time. However, the secondary colonies provided an additional pool of potential learners and allowed string pulling to continue to spread beyond these potential limitations.

There was also limited evidence to suggest that the learners from the secondary colonies were less proficient than those from the primary colonies. There was no significant difference between the overall proficiency of learners from primary and secondary colonies (Fig. 3c, Table S13), although there was a decline in overall learner proficiency between phases I and II. Particularly in the later stages of the experiment, competition over the limited number of flowers available may have prevented naïve bees from having the chance to learn, or to demonstrate their proficiency. As the number of knowledgeable bees increased, the relative contribution of each individual to the total number of string-pulling events per day decreased, but the starkest difference in performance was found among 'early' learners: those that first acquired string pulling in the early days of the experiment. These early learners, facing less competition for flowers, were able to rack up large numbers of string-pulling events without being inhibited by other knowledgeable bees at the start of the experiment, setting a higher 'baseline' number of string-pulling events for themselves that then came down.

It is unlikely that the decrease in proficiency was linked to any decay in the integrity of string-pulling transmission over multiple learning events. In colonies C1/SC1 and C3/SC3, the original trained demonstrators from C1 and C3 remained actively pulling throughout phases I and II. However, in colony C2, the demonstrator ceased string pulling after the first day of phase I (Fig. S6, Table S2). This meant that all learners from the corresponding secondary colony SC2 were only ever exposed to bees that, while knowledgeable, were not trained to perform string pulling by the experimenters. Still, learners o71 and o67 from colony SC2 went on to become the most proficient of all learners from secondary colonies, string pulling 745 and 183 times, respectively, during phase II (Fig. S2, Table S2). Taken together, the root cause of this decline in proficiency appears to have been the 'artificial ceiling' imposed by the number of strings available for the bees to pull in our experimental set-up, and the consequences of this, rather than string pulling failing to be properly transmitted across multiple generations of learners.

In our control colonies, which had no seeded demonstrators, fewer bees learned than in the matched experimental colonies. However, some did learn. Just two bees from a single control colony met the learning criterion, with the most proficient of these performing string pulling 18 times. Similar phenomena have also been observed in previous dyadic experiments on string pulling (Alem et al., 2016), as well as in open diffusion experiments involving a single-step puzzle box (Bridges et al., 2023). This does not preclude string pulling from having spread via social learning within our paradigm: significantly more bees learned in the experimental colonies (Fig. 2a). However, it serves to highlight yet again the astonishing behavioural flexibility of bumble bees. Repeatedly, across different non-natural foraging problems, bumble bees manage to 'innovate' their own solutions without any demonstration or training: but not all bees. Determining what makes these particular individuals innovate, while others fail to do so, would be a fascinating route for future studies. Such innovators may represent 'keystone individuals', acting as a source of novel behaviours or behavioural variants that can later become traditional within a population (Arbilly, 2018).

Innovation, 'a process that results in new or modified behaviour and that introduces novel behavioural variants into a population's repertoire' (Reader & Laland, 2003, p. 14), is a key component of animal culture. If culture refers to learned rather than innate behaviours then it follows that, at some point, someone had to perform the behaviour in question for the very first time. At least the first bee to learn string pulling in our control colony CC3, bee g21, can be said to have innovated string pulling (and may have served as a demonstrator for the subsequent learner, o94, which acquired string pulling the following day). The presence of these control learners does pose an interesting question: if the experiment had run for longer, could more bees in colony CC3 have learned string pulling? It is certainly possible. In previous control diffusion experiments using a puzzle box, which ran for 12 days, as many as nine bees learned (albeit with significantly lower proficiency than learners exposed to a demonstrator; Bridges et al.,

2023). In the present study, the proficiency of control learners was not significantly lower than that of experimental learners, although this could have been due to the very small sample size for the control learners ($N = 2$) and substantial variation among the experimental learners. While it seems likely that string pulling could have continued to spread to more bees in colony CC3, given more time, it is unclear whether it would be performed with a similar degree of frequency as seen in the experimental colonies.

To conclude, the results of our study confirm that, when given opportunity, bumble bees can innovate novel behaviours, can socially learn these behaviours and also have the ability to transmit and acquire these behaviours beyond colony limitations. The opportunity to practise and perform a behaviour, which can be inhibited by competition from other knowledgeable individuals when resources are limited, may also be key. However, the question as to whether similar novel, local behavioural adaptations occur among wild bumble bees remains open. Nectar robbing and its handedness (Goulson et al., 2013) may represent one potential example. Yet, with this and previous studies (Alem et al., 2016; Bridges et al., 2023), we have shown a clear and replicable tendency for bumble bees to develop their own local behavioural adaptations, which spread via social learning, if they are given the opportunity. If they fail to do so in the wild, therefore, this would suggest a lack of need or opportunity rather than any fundamental capacity.

Author Contributions

Olga Procenko: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Alice D. Bridges:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Conceptualization. **Amelia Kowalewska:** Investigation. **Mikko Juusola:** Writing – review & editing, Funding acquisition. **Lars Chittka:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

Data Availability

Data underlying the figures presented in the manuscript are available at https://figshare.com/articles/dataset/_/29612009.

Declaration of Interest

The authors have no competing interests to declare.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123439.

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