RESEARCH ARTICLE

Spontaneous quantity discrimination of artificial flowers by foraging honeybees

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ABSTRACT

Many animals need to process numerical and quantity information in order to survive. Spontaneous quantity discrimination allows differentiation between two or more quantities without reinforcement or prior training on any numerical task. It is useful for assessing food resources, aggressive interactions, predator avoidance and prey choice. Honeybees have previously demonstrated landmark counting, quantity matching, use of numerical rules, quantity discrimination and arithmetic, but have not been tested for spontaneous quantity discrimination. In bees, spontaneous quantity discrimination could be useful when assessing the quantity of flowers available in a patch and thus maximizing foraging efficiency. In the current study, we assessed the spontaneous quantity discrimination behaviour of honeybees. Bees were trained to associate a single yellow artificial flower with sucrose. Bees were then tested for their ability to discriminate between 13 different quantity comparisons of artificial flowers (numeric ratio range: 0.08–0.8). Bees significantly preferred the higher quantity only in comparisons where '1' was the lower quantity and where there was a sufficient magnitudinal distance between quantities (e.g. 1 versus 12, 1 versus 4, and 1 versus 3 but not 1 versus 2). Our results suggest a possible evolutionary benefit to choosing a foraging patch with a higher quantity of flowers when resources are scarce.

KEY WORDS: *Apis mellifera*, Approximate number system, Numeric, Object file system, Ratio, Subitizing

INTRODUCTION

Spontaneous quantity discrimination is the ability of animals to discriminate between two or more sets of items differing in magnitude, without specific training on any numerical task (Agrillo and Bisazza, 2014). This ability of animals to discriminate between quantities can be vital for survival in terms of avoiding predation (e.g. shoaling behaviour), determining the available food or predicting the outcome of aggressive group interactions, among others.

Spontaneous quantity discrimination is well studied in schooling fish because of their strategy of shoaling with larger groups of conspecifics to increase their chances of survival during a predation event. Mosquitofish and angelfish can discriminate between shoals differing by one when the group consists of four or fewer fish (1 versus 2, 2 versus 3, 4 versus 4), but they are able to differentiate between groups of conspecifics over four only when the ratio is at least 1:2 (e.g. 4 versus 8, 4 versus 12) (Agrillo et al., 2007, 2008; Dadda et al., 2009; Gómez-Laplaza and Gerlai, 2011a,b). This phenomenon is probably due to the theorized systems which animals use to process numerical tasks. For quantities of four and fewer, many animals use the object file system (OFS) or subitizing, where they keep track of each object individually (Agrillo et al., 2008; Kaufman et al., 1949; Piazza et al., 2002; Revkin et al., 2008; Rugani et al., 2013; Tomonaga and Matsuzawa, 2002; Trick and Pylyshyn, 1994). For quantities of four and more, animals use the analogue magnitude system (AMS) or approximate number system (ANS; Agrillo et al., 2008; DeWind et al., 2015; Feigenson et al., 2004; Rugani et al., 2013; Vallortigara, 2017) which fits with Weber's Law (Akre and Johnsen, 2014; Weber, 1978): Weber's Law allows animals to differentiate between two quantities based on their magnitudinal differences. For example, it is easier to differentiate 20 versus 40 fish compared with 20 versus 21 fish because of their magnitudinal differences. Other animals also demonstrate thresholds of spontaneous quantity discrimination in the AMS range. For example, salamanders demonstrate spontaneous quantity discrimination when choosing prey quantities in the AMS range of 8 versus 16 (ratio of 1:2) but not 8 versus 12 (ratio of 2:3) (Krusche et al., 2010). However, there are also species differences: North Island robins can spontaneously discriminate quantities of 7 versus 8 (ratio of 1:1.14) (Garland et al., 2012), and Prosimian primates were able to discriminate food item ratios of 1:3, such as 4 versus 12, when quantities were in the AMS range (Jones and Brannon, 2012). This suggests that despite an apparent common subitizing limit in animals (Agrillo et al., 2008; Howard et al., 2019c), there are environmental factors influencing how animals process numbers extending into the AMS range.

Honeybees are a model insect species well suited for the study of visual learning because individuals can be trained and tested following protocols first developed by Karl Von Frisch (1914, 1967). Specifically, bees have become an ideal species for testing the numerical abilities of invertebrates as they demonstrate visual learning of complex relational and conceptual tasks (Avarguès-Weber and Giurfa, 2013; Dyer, 2012; Srinivasan, 2010; Zhang, 2006). Honeybees are able to learn rules and solve tasks in order to receive a reward of sugar water (sucrose) such as maze navigation (Collett et al., 1993; Zhang et al., 1996, 2000, 1999), size discrimination (Avarguès-Weber et al., 2014; Howard et al., 2017a,b), pattern discrimination (Efler and Ronacher, 2000; Giger and Srinivasan, 1996; Giurfa et al., 1999; Srinivasan et al., 1993; Stach et al., 2004; Zhang and Srinivasan, 1994) and human face

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recognition (Avargues-Weber et al., 2018; Avarguès-Weber et al., 2010b; Dyer et al., 2005), as well as rules of 'above versus below' (Avarguès-Weber et al., 2011), and 'same versus different' (Giurfa et al., 2001).

Honeybees are able to count up to four landmarks (Chittka and Geiger, 1995; Chittka et al., 1995; Dacke and Srinivasan, 2008) and match up to four elements (Gross et al., 2009) with appetitive conditioning. Appetitive conditioning consists of rewarding individuals for a correct choice and not rewarding them for an incorrect choice. Appetitive–aversive differential conditioning consists of rewarding an individual for a correct choice and providing an aversive outcome for an incorrect choice (Avarguès-Weber et al., 2010a; Chittka et al., 2003). When trained with appetitive–aversive differential conditioning, bees can learn the rules of 'greater than' and 'less than' with the quantities 0–6, quantitatively value zero numerosity (Howard et al., 2018a), discriminate between quantities in the OFS and AMS range (Bortot et al., 2019a; Howard et al., 2019c), perform simple addition and subtraction with quantities 1–5 (Howard et al., 2019a; Howard et al., 2019b), transfer discrete numerical values to continuous size tasks (Bortot et al., 2019b preprint) and match small quantities of 2 or 3 with symbolic characters (Howard et al., 2019d). Recently, the difference in numeric discrimination when bees were trained with appetitive-only or with appetitive–aversive differential conditioning was investigated (Howard et al., 2019c); it appears that bees perform significantly better when trained using the latter. This study suggests that attention modulation may be a component of learning numerosity in animals (Avarguès-Weber et al., 2010a; Dyer et al., 2019). When trained with appetitive–aversive conditioning, honeybees were able to discriminate the quantities of 4 versus 8, 4 versus 7, 4 versus 6, and even 4 versus 5 (Howard et al., 2019c). In ecologically relevant situations, honeybees may use numerical assessments to choose where to forage based on flower number (Caraballo-Ortiz et al., 2011) and to evaluate conspecific number (Lowell et al., 2019). Despite the growing research on honeybee numerical ability (Dacke and Srinivasan, 2008; Giurfa, 2019a,b; Skorupski et al., 2018), spontaneous quantity discrimination in honeybees has not yet been formally tested, although studies allude to numerical use in natural environments (Caraballo-Ortiz et al., 2011; Lowell et al.,

2019). Honeybees are an important pollinator; therefore, understanding how numeric information is processed by these insects is of high interest.

In the current study, we determined whether honeybees preferred larger quantities of artificial flowers when associated with sucrose as a biologically relevant reward. Flower number has been identified as an important predictor of pollinator visits from the honeybee (Caraballo-Ortiz et al., 2011). Bees in the current study were first trained to associate a single yellow circle representing an artificial flower with a reward of sucrose. Bees were then shown two quantities of artificial flowers without the presence of a reward to determine whether they demonstrated any significant preferences for stimuli. We hypothesized that honeybees would prefer to visit a stimulus presenting a higher quantity of flowers if they could discriminate between the two quantities and identified more artificial flowers as being a higher quality source of nutrition.

MATERIALS AND METHODS
Study species
Experiments took place at the Johannes Gutenberg University Mainz, Germany, and the University of Melbourne, Australia, in 2018–2019. Honeybee foragers (*Apis mellifera*; Linnaeus, 1758) were collected from either gravity feeders providing approximately 10–30% by volume sucrose solution or directly from the hive entrances. Bees came from the managed hives of both universities. We tested 520 forager bees on their spontaneous preferences for larger or smaller quantities of artificial flowers and in control experiments.

Apparatus
Honeybees were individually recruited, trained and tested. Bees were trained to visit a rotating screen which presented four hangers at a time. We used a standard rotating screen (Avarguès-Weber et al., 2010b; Dyer et al., 2005) which was 50 cm in diameter and was made of a grey Plexiglas material containing hanger pegs (Fig. 1), which allowed hangers presenting stimuli to be attached. The hangers had landing platforms directly under stimuli where foragers could land to collect a drop of sucrose solution. The screen could be freely rotated between choices to randomize hanger position. Additionally, hangers could be moved between pegs to change their
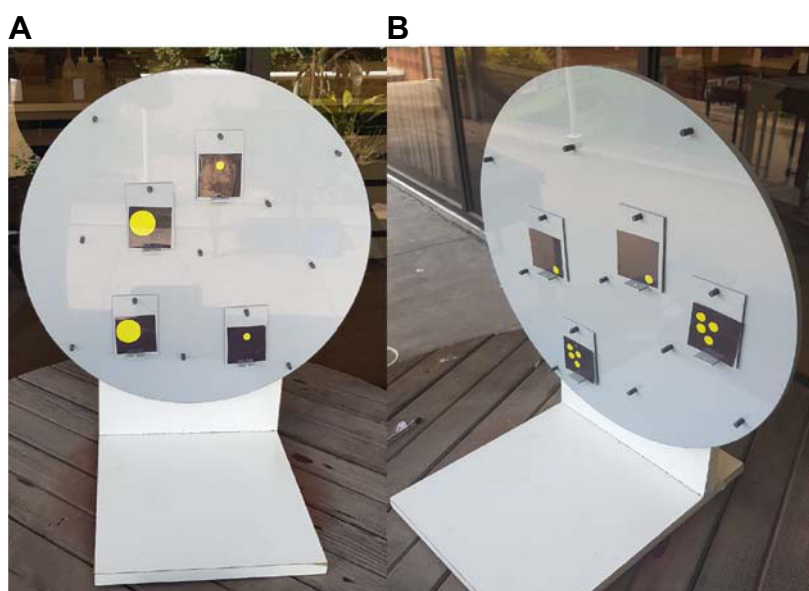

Fig. 1. The rotating screen apparatus used in the experiments. (A) The apparatus with examples of the priming stimuli presented. (B) The apparatus with examples of stimuli from the test of 4 versus 1 with equal element sizes.

position. Once a bee had made a choice and landed, it was allowed to finish drinking the sucrose on the landing platform before being collected onto a Plexiglas spoon with sucrose solution and placed behind an opaque screen while landing platforms, hangers and surrounding areas were cleaned with a 30% ethanol solution, then water, and dried. New stimuli were then presented on the hangers and the screen was rotated to randomize the position of stimuli before the bee made another choice or returned to the hive if satiated. Once it had finished imbibing sucrose, the bee could then fly out from behind the opaque screen to make a choice or, if satiated, could return to the hive.

Priming phase
Honeybee foragers were first trained to associate the artificial flower (yellow circle; Fig. 1A) with a reward of sucrose. Bees were trained to land on the hangers of the rotating screen to receive the sucrose reward. After bees learnt to individually land on the hangers, we placed ca. 10 μl drop of 25% sucrose solution on the hangers with one artificial flower directly above the landing platform containing the drop. Priming consisted of allowing bees to land and collect sucrose from the hangers, each presenting a single yellow circle of differing size (six possible sizes from 1 to 10 cm^2) (Fig. 1A). The size of the priming stimuli could be pseudo-randomly changed while the bee, once satiated, periodically returned to the hive (after approximately 2–6 choices known as a 'bout'). Once bees had made 20 landings to drink sucrose, thus associating the yellow circles with sucrose solution, they were given tests to determine whether they would prefer to visit the larger amount of artificial flowers when given the option between two quantities of circles.

Testing phase: quantity comparisons
Bees were tested for their preferences in 13 different quantity comparisons (Table 1, Fig. 2) in the absence of reinforcement (sucrose). One group was tested using stimuli which had an overall equal surface area of yellow colour (10 cm^2) regardless of element quantity and one group was tested using stimuli in which all individual elements were of equal size (all elements were 1 cm^2). Low level cues such as surface area, convex hull, line length and density are present when bees are foraging at flower patches. These

non-numerical cues are correlated with increasing quantity and would be available to naturally foraging bees; thus, we tested two conditions (surface area controlled or individual element size controlled) to begin to understand which cues bees may use for quantity tasks.

Honeybees prefer to visit larger flowers (Martin, 2004) and have preferences for specific shapes of flowers (Howard et al., 2018b; Lehrer et al., 1995), which may impact their choice of stimuli. Thus, the spatial arrangement of elements was randomized to account for this and different procedures were implemented to determine whether they preferred larger stimuli (e.g. preference for lower quantities with larger stimuli in the equal surface area condition). This was done by testing each comparison with stimuli where there was an equal overall surface area of elements or where stimuli contained elements of the same size. If bees preferred larger artificial flowers, they should choose the lower number in the equal surface area condition, as these stimuli would have fewer elements with larger areas. If bees preferred a larger area of yellow, then they should consistently choose the larger number when elements were the same size.

Each bee performed only one test comparison. The comparison which the bee was tested on was pseudo-randomly assigned and each test lasted for an unrewarded 10 choices each. Bees generally made 10 choices (landings/touches of a hanger or stimulus) in a row without returning to the hive during the test (which took approximately 1 min).

Testing phase: control experiments
Five different control experiments were conducted to ensure bees associated the yellow circle with sucrose solution and considered it as a rewarding 'flower' (Fig. 2). These control experiments contained a priming phase of 20 landings and a testing phase of 10 unrewarded choices.

During the first experiment (control 1; n=50), bees were primed on the yellow circles, as above, and then tested on the comparison between a 6×6 cm yellow square versus a 6×6 cm grey square to determine whether they had a preference for the colours used in the experiment after the same priming to artificial flowers.

During the second control experiment (control 2; n=10), bees were primed on the yellow circles, as above, and then tested on the comparison between a 6×6 cm grey card and 6×6 grey card containing a single yellow circle. This would determine whether bees preferred the yellow circle over the grey card and thus associated the yellow circle with the reward.

During control experiments 3–5, bees were primed to 6×6 cm sand-blasted grey aluminium stimuli, then tested on 1 versus 12 (equal surface area stimuli; control 3; n=34), 4 versus 1 (equal surface area; control 4; n=10) or 4 versus 1 (equal element size; control 5; n=12) to determine whether the priming to the single artificial flower was driving any preferences observed for quantities of artificial flowers. These control experiment comparisons were chosen as these tests in the quantity comparison phase of the experiments yielded significant results (see Table 2).

Statistical analysis
Ten choices per bee were recorded during the test and then analysed. Each bee received a score out of 10 for the number of 'correct choices' defined per stimulus comparison. To determine whether bees demonstrated a significant preference for a stimulus during the non-rewarded tests, we tested whether the mean number of 'correct choices' observed for each comparison was significantly different from chance. We analysed data with a generalized linear

Table 1. Quantity comparisons and their ratios, system range and number of bees tested per group

Quantity	Numeric ratio	Ratio	OFS or AMS	No. of bees tested	
				Equal surface area	Equal element size
1 vs 12	0.08	1:12	Both	15	25
4 vs 20	0.20	1:5	AMS	18	27
1 vs 4	0.25	1:4	OFS	10	15
1 vs 3	0.33	1:3	OFS	12	12
4 vs 12	0.33	1:3	AMS	11	12
1 vs 2	0.50	1:2	OFS	12	12
2 vs 4	0.50	1:2	OFS	30	15
4 vs 8	0.50	1:2	AMS	13	10
4 vs 7	0.57	1:1.75	AMS	12	11
2 vs 3	0.67	1:1.5	OFS	12	12
4 vs 6	0.67	1:1.5	AMS	22	17
3 vs 4	0.75	1:1.33	OFS	30	15
4 vs 5	0.80	1:1.25	AMS	12	12

OFS, object file system; AMS, analogue magnitude system. Bees in the equal surface area group were tested with stimuli which had an overall equal surface area of yellow colour (10 cm^2) regardless of element quantity; bees in the equal equal element size group were tested with stimuli in which all individual elements were of equal size (all elements were 1 cm^2).
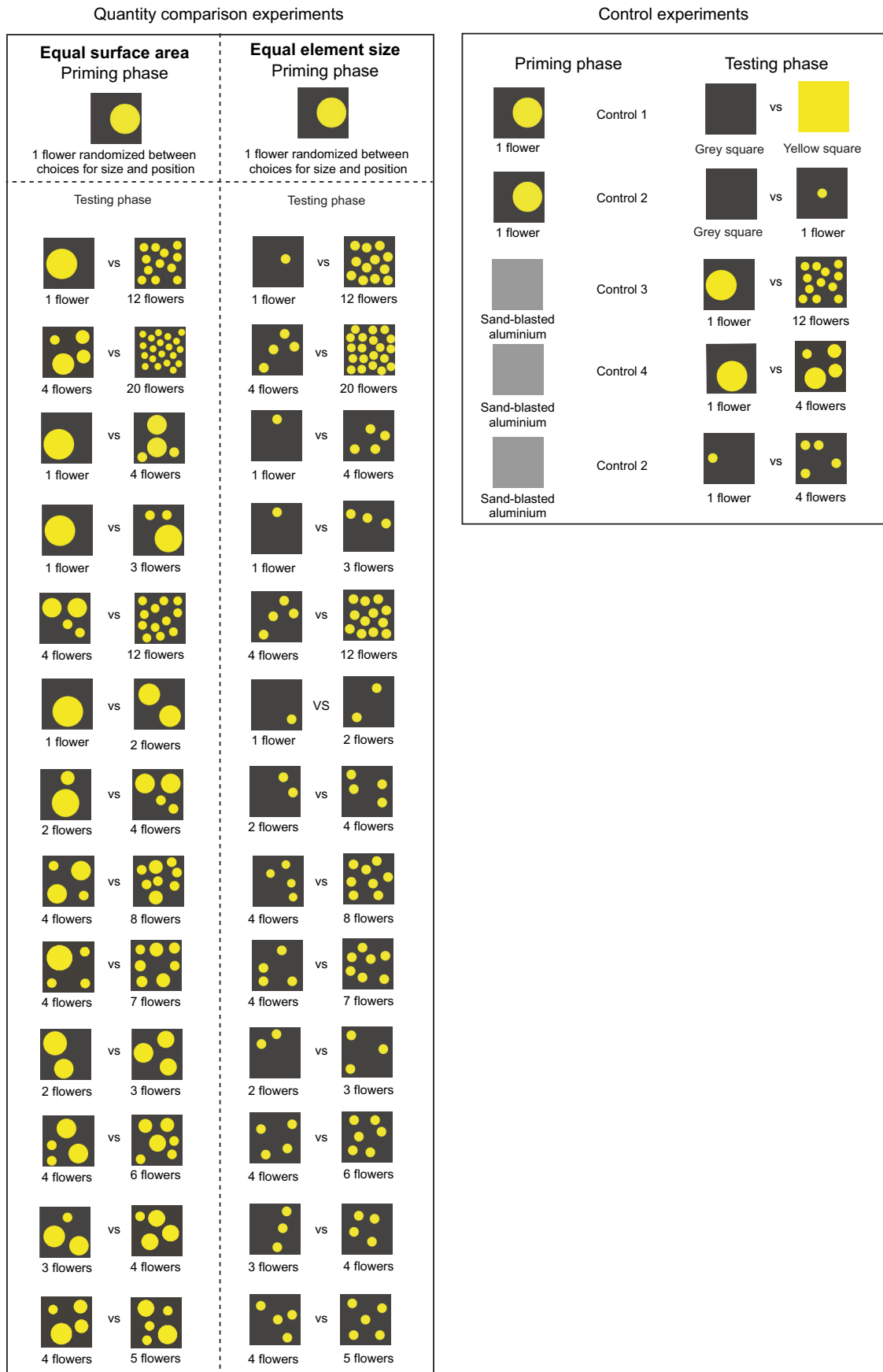
Fig. 2. Examples of the stimuli used for all 13 quantity comparisons and 5 control experiments.

Table 2. Preferences for the higher number of elements using stimuli with either an overall equal surface area or an equal element size across 13 quantity comparisons

Ratio	Quantity	Equal surface area				Equal element size			
		Proportion	z-value	P-value	CI	Proportion	z-value	P-value	CI
0.08	1 vs 12	0.60	2.112	0.035*	0.507; 0.664	0.70	4.849	<0.001*	0.596; 0.713
0.20	4 vs 20	0.50	−0.745	0.456	0.400; 0.545	0.50	0.122	0.903	0.444; 0.563
0.25	1 vs 4	0.61	2.182	0.029*	0.513; 0.702	0.62	2.91	0.004*	0.541; 0.695
0.33	1 vs 3	0.575	1.637	0.102	0.486; 0.661	0.61	2.354	0.019*	0.519; 0.693
0.33	4 vs 12	0.50	−0.762	0.446	0.372; 0.557	0.40	−1.275	0.202	0.355; 0.531
0.50	1 vs 2	0.50	0.000	1.000	0.411; 0.589	0.53	0.730	0.466	0.444; 0.621
0.50	2 vs 4	0.49	−0.346	0.729	0.434; 0.546	0.51	0.163	0.870	0.427; 0.586
0.50	4 vs 8	0.50	−0.701	0.483	0.445; 0.615	0.50	−0.600	0.549	0.374; 0.568
0.57	4 vs 7	0.475	−0.547	0.584	0.387; 0.564	0.50	0.191	0.849	0.416; 0.601
0.67	2 vs 3	0.417	−1.817	0.069	0.331; 0.506	0.56	1.275	0.202	0.469; 0.645
0.67	4 vs 6	0.468	−0.943	0.346	0.403; 0.534	0.50	−0.307	0.759	0.414; 0.563
0.75	3 vs 4	0.51	0.346	0.729	0.454; 0.566	0.53	0.816	0.415	0.453; 0.612
0.80	4 vs 5	0.50	−0.365	0.715	0.395; 0.572	0.50	0.183	0.855	0.419; 0.597

Shown is the proportion of choices for the larger quantity and corresponding P-values for each test. Asterisks indicate significance (*P<0.05). CI, 95% confidence interval.

mixed-effects model (GLMM) with a binomial distribution using the 'glmer' package within the R environment for statistical analysis (http://www.R-project.org/). This was done by fitting individual GLM models to response data for each treatment including only the intercept term as a predictor.

RESULTS
Testing phase: quantity comparisons
Honeybees were tested for their ability to spontaneously discriminate between sets of artificial flowers differing in number after training to a rewarding single artificial flower. Bees were tested on 13 different quantity comparisons using two sets of stimuli with either an overall equal surface area of elements or where all elements were of equal size (Table 1). Honeybees demonstrated a significant preference in five comparisons. Bees preferred the higher quantity of four flowers in 61.0% of choices when shown 1 versus 4 (statistical test: logistic regression tested differences between observed proportion of bee choices and chance level, $y=0.5$; $z=2.182$, $P=0.029$, $n=10$; Table 2) in the equal overall surface area condition. Bees also preferred the higher quantity of four in 62.0% of choices when presented with 1 versus 4 ($z=2.910$, $P=0.004$, $n=15$; Table 2) in the equal element size condition. Bees preferred the higher quantity of 12 in 60.0% of choices in the 1 versus 12 equal surface area comparison ($z=2.112$, $P=0.035$, $n=15$; Table 2) and in the equal element size condition in 70.0% of choices ($z=4.849$, $P<0.001$, $n=25$; Table 2). In the 1 versus 3 comparison, where all elements were of an equal size, bees preferred the higher quantity of three in 60.8% of choices ($z=2.354$, $P=0.019$; Table 2).

Testing phase: control experiments
For the control, we tested whether bees had a preference for the colours used in the quantity experiments (grey versus yellow), whether they preferred our artificial flowers to the background of grey, and then whether our priming phase had an effect on bee performance in choosing the higher quantity of elements in the 4 versus 1 and 12 versus 1 experiments (Table 2). We used a selection of quantity comparisons in which bees had been successful during the quantity comparison experiments. In the control 2 experiment, bees preferred the single artificial flower compared with the grey square in 79.0% of choices ($z=5.397$, $P<0.001$, $n=10$; Table 3). In all other conditions, honeybees demonstrated no significant preference for a quantity or stimulus (see Tables 2 and 3). Thus, without priming to a single artificial flower, bees demonstrated no quantity preferences in the 4 versus 1 and 12 versus 1 conditions.

DISCUSSION
Honeybee foragers were trained to associate a drop of sucrose with a yellow circle representing an artificial flower. Bees were then separately tested on their preference for larger quantities of artificial flowers considering two conditions: (i) where all stimuli containing artificial flowers had the same surface area of yellow, and (ii) where all artificial flowers were of the same size. Honeybees demonstrated a preference for the higher quantity of flowers in the 1 versus 4 and 1 versus 12 tests across both groups, and in the 1 versus 3 comparison where all elements were of an equal size. All other tested numerical combinations yielded results that were not significantly different to chance expectation (Table 2). Bees appear to spontaneously prefer the larger quantity when compared with one element, but have no preference for other quantity comparisons. Additionally, the ratio between the lower and higher quantity of flowers must be at least 1:3 (0.33), as bees failed to show a preference in the 1 versus 2 comparison. The lack of significant preferences in most of the comparisons (a) may be due to bees having no preference for these greater or lesser quantities, or (b) may be a result of bees being unable to discriminate between the quantities. These potential explanations are discussed below.

Table 3. Preferences for the yellow card (control 1), the yellow circle (control 2) or the higher quantity (control 3–5)

Control	Comparison	Percentage	z-value	P-value	CI
1	Grey versus yellow	0.518	0.805	0.421	0.474; 0.562
2	Grey versus yellow circle	0.790	5.397	<0.001*	0.703; 0.862
3	1 vs 12 (equal surface area)	0.450	−1.841	0.066	0.398; 0.503
4	1 vs 4 (equal surface area)	0.500	0.000	1.000	0.393; 0.587
5	1 vs 4 (equal element size)	0.490	−0.200	0.841	0.411; 0.589

Asterisks indicate significance (*P<0.05).

The results of the control experiments (Table 3) demonstrate that bees did learn the yellow circle as an artificial flower providing a reward during the priming phase. When primed using the same stimuli as the main experiments (primed to differently sized yellow circles), bees showed no significant preference for yellow or grey colours (control 1); however, they demonstrated a significant preference for a yellow circle on a grey background versus a grey square stimulus (control 2). These two experiments show that bees do not prefer the yellow colour alone – it is the yellow circle (artificial flower) which drives a preferential choice in the control experiments and thus the quantity comparisons. This finding is strengthened by examining the results from control experiments 3–5, where bees were primed to sand-blasted aluminium cards and tested on quantity comparisons 1 versus 4 and 1 versus 12. Despite showing a significant preference for the greater quantity in the main experiments when primed with the yellow circle, bees had no preference for these quantities when they had not associated the yellow circle with a reward of sucrose. These results also suggest that any significant preference for higher quantities was due to the association of a single artificial flower with sucrose.

Results from the 1 versus 3, 1 versus 4 and 1 versus 12 tests suggest that bees can discriminate between some pairs of quantities, and thus may associate larger quantities with potentially more artificial flowers to forage on, but this preference is not evident when both quantities are larger than 1 or in the case of 1 versus 2. The results indicate that bees are either unable or not motivated to discriminate between higher quantities without specific training on the task. Bees did not show a preference for larger quantities above 4 even at a relatively large magnitudinal difference (ratio of 1:5 in the 4 versus 20 comparison). Additionally, the results from the tests of 1 versus 3 suggests that bees may use overall surface area to discriminate between quantities when the comparison is challenging, such as a preference for a larger surface area. Bees did not significantly prefer the higher quantity of 3 (1 versus 3) when the stimuli were controlled for overall surface area but did demonstrate a preference when the larger number had a greater surface area (in the equal element size condition). This same trend was not present in the results of 1 versus 4 or 1 versus 12, which are less challenging quantity comparisons, thus suggesting that more challenging comparisons of quantity may lead to low-level cues being used by bees.

Flower number in a foraging area has a strong influence on the number of visits from pollinators such as the honeybee (Caraballo-Ortiz et al., 2011). Our current study provides an important new insight into the relevance of quantity comparisons during natural foraging bouts on real flowers. For example, it may not be important for bees to differentiate between two or more flowers as they may simply classify these quantities as 'many'. When foraging, perhaps there is little difference between visiting a flower patch which provides two flowers to visit as opposed to three or four. However, when conditions are not optimal and few flowers are present in an environment, it may be vitally important to find a patch with more than one flower. For example, Gómez-Laplaza and Gerlai (2011a,b) suggest that in fish, the inability to discriminate between shoals consisting of 5 versus 3, 8 versus 5, 9 versus 6, or 6 versus 4 conspecifics may be because the choice for a larger shoal would not significantly increase an individual's chance of survival. Furthermore, the magnitude may need to be greater between two shoals in order for there to be a significant advantage to choosing the larger shoal. The same may be true for honeybees when choosing a flower patch.

Alternatively, the potential inability of bees to discriminate between quantities of artificial flowers could be due to the limit of

selective attention in honeybees during spatial visual tasks (Morawetz and Spaethe, 2012). The search mechanism during spatial tasks for honeybees has been identified as 'serial search', the successive processing of each object during a search task for a target among distractors for which spatial attention is necessary. During serial search, as the number of targets is increased, errors and search time typically decrease, while as the number of distractors increases, error rate and search time increase (Holmgren et al., 1974; Morawetz and Spaethe, 2012; Treisman and Gelade, 1980). This is in contrast with 'parallel search', where all objects presented are processed at the same time, and thus error rate and search time are not dependent on the number of targets or distractors present (Morawetz and Spaethe, 2012). Honeybees are known to use serial search, and this mechanism of visually searching for a target could have influenced our results. Perhaps the number of elements contained within the alternative stimuli during tests was too high for bees to process the visual task efficiently, leading to errors and/or a tendency to choose at random.

The inability of bees to spontaneously discriminate between quantities above 4 may also be due to a lack of adaptive value. Agrillo et al. (2008) proposes that while female mosquitofish had difficulty with ratios in the AMS range, such as 4 versus 5, 4 versus 6, 4 versus 7, 5 versus 6, 6 versus 7, 6 versus 8, 7 versus 8, and 8 versus 12, this is not an uncommon phenomenon across species, suggesting a neural processing constraint for quantity discrimination. Six-month-old human infants are able to discriminate between large numbers such as 8 versus 16, but not 8 versus 12 (Xu and Spelke, 2000) while 10-month-old infants can discriminate between 8 versus 12 but not 8 versus 10 (Xu and Arriaga, 2007), which suggests evidence of experience improving quantity discrimination. Cotton-top tamarins can perform spontaneous number discriminations of 4 versus 8, 4 versus 6 and 8 versus 12, but fail at discriminations of 4 versus 5 and 8 versus 10 comparisons (Hauser et al., 2003). Mosquitofish, cotton-top tamarins and human infants are all able to discriminate quantities above 4 when the ratio is less challenging, but fail at some more difficult comparisons. The above comparative studies suggest that an ability to compare quantities using approximate magnitudes is phylogenetically old and the evolution of this skill may predate the divergence of major vertebrate classes (Agrillo et al., 2008; Rugani et al., 2013). The ability to spontaneously discriminate between quantities of 2 and more is not present in honeybees in this study. However, studies show that with appetitive–aversive conditioning, honeybees can discriminate between challenging ratios of 0.80 (4 versus 5) and classify the quantities 0–6 as 'greater' or 'lesser' in the context of other quantities (Howard et al., 2018a, 2019b,c), suggesting that an ability to process and discriminate quantities within the OFS and AMS ranges is not out of reach for insects, even if it may not be a spontaneous behaviour at least in the context of foraging.

Honeybees have evolved in tropical environments, which host scarce but clustered sources of nutrition (Donaldson-Matasci and Dornhaus, 2012; Dornhaus and Chittka, 2004b). Thus, honeybees may have acquired a fast but inaccurate visual search strategy when compared with bumblebees (Morawetz and Spaethe, 2012), which have evolved in sparse but evenly distributed resource environments in temperate zones (Dornhaus and Chittka, 2004a). Consequently, bumblebees use a slow but careful foraging strategy (Dornhaus and Chittka, 2004a; Morawetz and Spaethe, 2012). The fast but error-prone strategy of honeybees is useful for environments where accuracy provides no benefit (Morawetz and Spaethe, 2012). The example given by Morawetz and Spaethe (2012) is a tree full of identically blooming flowers, where there are many targets and few

distractors; thus, being fast and inaccurate will yield more nectar collection than being slow and accurate. Honeybees may have evolved to discriminate between sparse and abundant resources such as flower number (e.g. 1 versus 12 or 1 versus 4 or 1 versus 3 flowers in our study), but the need to differentiate within those categories of sparse or abundant flower quantity is not ecologically beneficial. For example, the need to discriminate between one flower and multiple flowers may be a useful skill for honeybees when resources are sparse, but the need to differentiate between patches containing multiple flowers will not yield greater nectar collection if bees are accurate and slow rather than inaccurate but fast; thus, finer discrimination is not evolutionarily beneficial. Additionally, for honeybees viewing the stimuli on the rotating screen, the artificial flower acted as the target, and thus when there were many targets (e.g. 4 versus 20, 4 versus 12, 4 versus 8), which were clustered relatively close together (within a 50 cm diameter circle), there was a lower pressure for bees to choose greater quantities of the targets, as all individual elements are targets.

Invertebrates including mealworms, ants and now honeybees in the present study have been tested for their spontaneous quantity discrimination ability (Carazo et al., 2012, 2009; Cronin, 2014; Wittlinger et al., 2006). A prominent question in the area of animal numerical ability is how species without mammalian or avian brains represent quantity and numerosity in the brain (Giurfa, 2019b; Nieder, 2016). It is difficult to examine the brain function of invertebrates during complex tasks, such as spontaneous quantity discrimination. As mealworms, ants and honeybees have an innate sense of quantity, other invertebrates for which there are sophisticated neural analysis techniques (e.g. *Drosophila*: Roman and Davis, 2001; Wolf et al., 1998) could be tested for the same spontaneous number use. It could thus be possible to determine which part of the brain is associated with numerical ability and what structures, genes and neurons may be involved. Such experiments would shed light on this major question in the field of invertebrate numerical cognition and the evolution of number sense.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: S.R.H., A.G.D.; Methodology: S.R.H., A.G.D.; Validation: J.S.; Formal analysis: S.R.H., J.E.G.; Investigation: S.R.H., J.S., L.N., A.G.D.; Resources: S.R.H., J.S., A.G.D.; Data curation: J.E.G.; Writing - original draft: S.R.H.; Writing - review & editing: S.R.H., J.S., J.E.G., L.N., A.A.-W., A.D.G., A.G.D.; Visualization: A.G.D.; Supervision: S.R.H., J.S., A.G.D.; Project administration: S.R.H., J.S., A.G.D.; Funding acquisition: S.R.H., J.S., A.G.D.

Data availability
All raw data are available from the Dryad Digital Repository (Howard et al., 2020): dryad.kwh70rz0w

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