

Bumblebees gain fitness through learning

Nigel E. Raine^{1,2} and Lars Chittka¹

¹ School of Biological and Chemical Sciences, Queen Mary, University of London, Mile End Road, London, E1 4NS, UK

² Author for correspondence (n.e.raine@qmul.ac.uk).

Summary

Despite the widespread assumption that the learning abilities of animals are adapted to the particular environments in which they operate, the quantitative effects of learning performance on fitness remain virtually unknown. Here we evaluate the learning performance of bumblebees (*Bombus terrestris*) from multiple colonies in an ecologically relevant associative learning task under laboratory conditions, before testing the foraging performance of the same colonies under the field conditions. We demonstrate that variation in learning speed among bumblebee colonies is directly correlated with foraging performance, a robust fitness measure, under natural conditions. Colonies vary in learning speed by a factor of nearly 5, with the slowest learning colonies collecting 40% less nectar than the fastest learning colonies. Such a steep fitness function suggests strong selection for higher learning speed in bumblebees. Demonstrating the adaptive value of differences in learning performance under the real conditions in which animals function represents a major step towards understanding how cognitive abilities of animals are tuned to their environment.

Keywords: adaptive value, associative learning, flower colour, foraging behaviour, learning speed, nectar collection

1. INTRODUCTION

Learning, or the adaptive modification of behaviour based on experience, affects virtually every aspect of animal behaviour. However, despite the abundance of research on the mechanisms of learning in a wide variety of animal taxa, we still know very little about how learning performance is actually adapted to real ecological conditions (Shettleworth 1998; Dukas 2004). As different individuals or species vary widely in their learning capacities, it is

commonly assumed that these differences reflect adaptations to the natural conditions under which such animals operate (Gallistel 1990; Dukas 1998; Shettleworth 1998). Whilst it is intuitively appealing to assume that such variation in learning performance is adaptive (Johnston 1982; Dukas 1998), few studies have yet been conducted to specifically examine this link under natural conditions.

Laboratory studies, using grasshoppers (Dukas & Bernays 2000) and parasitoid wasps (Dukas & Duan 2000), suggest that animals able to form associations between cues (such as colour, odour or location) and rewards perform better than animals prevented from learning. Other laboratory studies, applying artificial selection to the learning ability of fruit flies, provide evidence for potential fitness costs associated with enhanced performance in associative learning (Mery & Kawecki 2003, 2004) or long term memory (Mery & Kawecki 2005) tasks. Whilst these results suggest that the ability to learn is useful (compared to being unable to learn) in highly controlled laboratory situations, and that enhanced learning appears to incur higher costs, they do not yet inform us directly about the potential fitness payoffs for animals with different learning abilities under natural conditions. Circumstantial evidence for the adaptive value of learning comes from between species comparisons (Dukas & Real 1991; Sherry & Healy 1998; Healy *et al.* 2005): for example, vole species with larger home ranges typically have better spatial memory, and their hippocampi (brain areas which store spatial memories) are typically larger (Sherry & Healy 1998). Whilst such studies suggest that learning performance and ecologically important measures (such as home range size) are correlated, the species compared also vary in numerous other ecological requirements. Therefore, to make further progress in understanding the evolutionary and ecological relevance of learning abilities, we must quantify how and to what extent learning differences within species affect animal fitness in nature (Papaj & Prokopy 1989; Dukas & Duan 2000).

Here, we directly link variation in learning performance with field foraging performance (a robust measure of fitness) for multiple bumblebee colonies (*Bombus terrestris*). In our laboratory learning trials, the bees' task was to overcome their innate preference for blue (Lunau *et al.* 1996; Chittka *et al.* 2004; Raine *et al.* 2006a) and learn to associate yellow as a predictor of floral reward. This is a simple associative task that bumblebees are able to learn, but individuals and colonies vary in their speed and accuracy (Chittka *et al.* 2004; Raine *et al.* 2006b). The task is ecologically relevant because foraging bees use a variety of cues, including floral colour, pattern and scent, to recognize, discriminate and learn the flowers from which they collect food (nectar and pollen) (Menzel 1985; Chittka & Raine 2006). As social insects, reproduction is restricted to subset of individuals within each bumblebee

colony. Hence intercolony (rather than inter-individual) variation in performance forms the raw material upon which any selection for learning ability could act.

2. MATERIALS AND METHODS

(a) *Learning performance*

We obtained 12 bumblebee (*Bombus terrestris dalmatinus*) colonies, each containing 30-40 workers, from Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands). Prior to experiments, bees were fed pollen and artificial nectar *ad libitum* without exposure to coloured stimuli associated with food. All workers were uniquely marked on the thorax with numbered, coloured tags (Opalith tags, Christian Graze KG, Germany). This allowed individuals to be accurately identified in both laboratory learning experiments and field foraging trials.

Bees were pre-trained to forage from 20 bicoloured, blue and yellow, artificial flowers in a laboratory flight arena. The square, bicoloured flowers were constructed from two halves (each 12 x 24 mm): one yellow (Perspex® Yellow 260) the other blue (Perspex® Blue 727). During pre-training all bicoloured flowers were rewarded with 50% (w/w) sucrose solution providing previously colour-naïve bees with an equal chance to associate both colours with reward (Raine *et al.* 2006b). Bees completing at least 5 consecutive foraging bouts on bicoloured flowers were selected for training. These foragers were trained individually, in a flight arena containing 10 blue (Perspex® Blue 727) and 10 yellow (Perspex® Yellow 260) artificial flowers (each 24 x 24 mm). Yellow flowers were rewarding (each contained 15µl of 50% (w/w) sucrose solution), whilst blue flowers were empty (unrewarding). Bees were regarded as choosing a flower when they either approached (inspected), or landed on it. Landing on a flower did not necessarily result in a feeding (probing) event. Therefore before probing a rewarding (yellow) flower, bees could choose both yellow/ rewarding or blue/ unrewarding flowers by approaching or landing on them (without probing). Choosing a yellow (rewarding) flower was regarded as 'correct', whilst choosing a blue (unrewarding) flower was deemed to be an 'error'. We recorded the choice sequence made by each bee from the time it first entered the flight arena. Recording the flower choices for each bee ceased once it had made 99 flower choices after the first time it probed a rewarding (yellow) flower (Raine *et al.* 2006b). Therefore each bee made at least 100 flower choices, including the first time it probed a rewarding flower, plus any choices made before this first probing event.

Flowers were changed and their positions re-randomized between foraging bouts to prevent bees using scent marks or previous flower positions as predictors of reward. Flower

colours were selected so that bees had to overcome their strong, unlearned preference for blue, before associating one of their innately least favoured colours (yellow) with reward (Chittka *et al.* 2004; Raine *et al.* 2006a). Fifteen bees were trained from each colony (i.e. 180 bees in total) between 4 and 24 July 2005. Thorax width measurements were taken for each of these bees as a measure of body size. Controlled illumination for laboratory experiments was provided by high frequency fluorescent lighting (TMS 24F lamps with 4.3 Khz ballasts, Philips, Netherlands fitted with Activa daylight tubes, Osram, Germany) to simulate natural daylight above the bee flicker fusion frequency.

(b) Learning curves

The starting point for each bee's learning curve was the proportion of errors made (blue flowers chosen) before the bee first probed a rewarding (yellow) flower. For bees making fewer than 5 flower choices (either by approaching or landing on them) before probing a rewarding flower ($n = 53$), we used the colony mean proportion of errors (calculated from bees making 5 or more such choices). Flower choices made by each bee after (and including) the first time it probed a rewarding (yellow) flower were evaluated as the number of errors (blue flowers chosen) in each group of 10 choices. Learning curves (first order exponential decay functions: $y = y_0 + Ae^{-x/t}$) were fitted to these eleven data points (i.e. the start pointing and subsequent 10 groups of ten flower choices) for each individual bee, using Microcal Origin® (Chittka *et al.* 2004; Raine *et al.* 2006b), to capture the dynamic nature of the learning process. Here, x is the number of flower choices the bee made, starting with the first time it probed a yellow flower, and y is the number of errors. The saturation performance level (y_0) is the number of errors made by a bee after finishing the learning process, i.e. when reaching a performance plateau. The decay constant (t) is a measure of learning speed: high values of t correspond to slow learning, whereas lower t values indicate faster learners. A is the curve amplitude: the maximum displacement (height) of the curve above y_0 . Both amplitude (A) and saturation performance (y_0) were constrained between 0-10 for curve fitting. Eight (out of 180) bees showed no appreciable improvement in performance during the task, and the software generated 'learning curves' that were essentially horizontal lines. These bees were excluded from subsequent analyses because their t values were either very high (>400) or negative.

To validate our curve fitting approach we reanalysed learning data using an alternative methodology. In this approach we assessed the number of flower choices taken by each bee

(after the first time it probed a yellow flower) to reach an 80% improvement in task performance from its starting level. Starting performance levels for each bee were calculated as above, whilst the final performance level was taken as the number of errors during the last 10 recorded flower choices. A 10 choice moving average was calculated across the 100 flower choices (including the first time a rewarding flower was probed) for each bee (i.e. choices 1-10, 2-11...91-100). The moving averages were compared sequentially against the 80% task improvement criterion. This provided the number of flower choices made by each bee before it reached its own 80% improvement criterion. We found a strong correlation between this 'curve-free' measure of learning speed and the t values generated from fitted learning curves (Pearson's correlation: $r = 0.484$, $n = 172$, $p < 0.005$). Thus bees determined as fast learners by curve fitting (i.e. those with low t values) also took fewer flower choices to reach their 80% improvement criterion. We therefore use t values as a robust measure of learning speed throughout this study.

(c) *Field foraging performance*

The nectar foraging performance of the same twelve colonies for which we had obtained learning performance data was assessed by allowing them to forage in the environment around Queen Mary College (E1 4NS, London, UK). Once outside the nest, bees could forage freely in an area containing large numbers of flower species in bloom growing in numerous private gardens, several large parks, and other areas of open land (e.g. canal or railway embankments). Therefore bees made the same foraging decisions they would face in more 'natural' habitats, namely where to forage and which flowers to visit in a diverse and abundant flower market whose resources are patchily distributed in space.

Foraging performance was measured for six colonies per day for twelve days between 25 July and 6 August 2005 (heavy rain prevented data collection on 27 July). Two sets of six colonies were assigned at the start of the experiment, and the performance of each set was assessed on alternating days (i.e. 6 colonies per day for 12 days = 72 colony days in total). On each day of data collection, all bees were allowed to leave test colonies from 09:00-17:00, after which data were recorded only for incoming bees until all returned or 19:00. Any bees returning later were reintroduced to their nest the following morning. For each colony, bee traffic was controlled by means of shutters in the entrance tube so that all exiting and returning foragers could be captured and weighed. As far as possible, all bees that wished to forage were allowed to do so. Observers monitored the time and mass of each individual forager when it departed, and returned to, the nest from each foraging bout. As they departed

and arrived, bees were captured in plastic vials and transferred to an electronic balance (Ohaus Navigator N20330, Ohaus Corporation, Pine Brook, NJ: accuracy $\pm 2\text{mg}$) to measure their body mass. Departure time was taken when the bees were released after weighing and the time of arrival when the bees first reappeared at the nest. Although individual foragers can collect nectar, pollen or both, the bees in this study collected predominantly nectar only. This was an intended result of providing all colonies with *ad libitum* pollen so that we could collect as large an amount of comparable nectar foraging data as possible. Observers measuring foraging rates were entirely blind to the learning performance of each colony as assessed in the first part of the experiment.

In bumblebees, the amount of food brought into the colony has a very strong influence on the output of sexually active offspring (males and new queens: Schmid-Hempel & Schmid-Hempel 1998; Pelletier & McNeil 2003; Ings *et al.* 2006), thus tightly linking colony foraging performance and reproductive output. As such foraging performance represents a robust proxy measure of fitness. We determined the foraging rate by dividing the difference in the forager's body mass (i.e. return minus outgoing mass) by the foraging trip duration (Ings *et al.* 2005, 2006). Nectar foraging rate was calculated on a per bout basis for each colony. This measure of performance is unaffected by differences in overall colony size or the number of foragers leaving each colony. If the rate of colony nectar collection is the same, it does not matter if this rate is achieved by 1 forager performing 30 bouts or 30 foragers each completing a single bout. As such we consider the foraging bout, rather than the individual forager, as the suitable unit of replication. To exclude orientation and defecation flights we considered only trips lasting more than 5 minutes as foraging bouts (Capaldi & Dyer 1999; Spaethe & Weidenmüller 2002). Under this criterion 40 (0.9%) trips were excluded, leaving 4394 foraging bouts (2843 hours of continuous foraging activity) for analysis.

3. RESULTS

We found significant variation among colonies in learning speed (t value: one way ANOVA: $F_{11, 160} = 1.900$, $p = 0.043$; figure 1). Differences in average learning speed between bees in these colonies were highlighted when we compared the number of flower choices taken to reduce the number of errors made by 80% from starting performance towards their saturation level (y_0 : i.e. move 80% of the way from the top to the bottom of their learning curve). On average, bees from the fastest learning colony (D19) took only 15 flower visits to achieve an 80% improvement in task performance (from starting error levels), whilst bees from the

slowest learning colony (D11) took 71 visits to reach the same performance criterion (figure 2). Therefore, these two colonies differed in learning speed by a factor of 4.7.

Nectar foraging rates of colonies allowed to forage under natural conditions varied significantly (one way ANOVA: $F_{11, 4382} = 17.87$, $p < 0.005$) with the most successful foraging colony bringing in almost three times more nectar than the least successful (means \pm 1 SEM = 257 ± 18 versus 87 ± 8 mg/hour).

Most importantly, we found a significant correlation between learning and foraging performance, such that on average colonies with higher learning speeds (lower t values) brought in more nectar per unit time (Pearson's correlation: $r = -0.588$, $n = 12$, $p = 0.044$; line of best fit: nectar foraging rate = $-2.65t + 255.95$; figure 3). As foraging performance represents a robust proxy measure of fitness, this correlation provides evidence that higher learning speed is closely associated with increased bumblebee colony fitness under natural conditions.

In other studies, worker body size has been shown to have a strong effect on foraging performance, with larger bees collecting proportionately more nectar (Spaethe & Weidenmüller 2002; Ings *et al.* 2005). Although the size of workers differed significantly among colonies in our study (thorax width from laboratory learning trials: one way ANOVA: $F_{11, 168} = 8.407$, $p < 0.005$; body mass of outgoing workers from field foraging trials: $F_{11, 592} = 18.276$, $p < 0.005$), we found no correlation between mean forager size and either learning speed (thorax width: $r = -0.383$; $n = 12$; $p = 0.220$) or foraging performance (body mass: $r = -0.011$; $n = 12$; $p = 0.972$) among the twelve colonies. Furthermore, the partial correlation between colony learning and foraging performance remains significant when the potential effects of variation in worker body size are removed (Partial correlation: $r = -0.641$, $n = 12$, $p = 0.034$). Thus colonies containing larger workers did not learn faster or collect more nectar in this study.

4. DISCUSSION

Our study assesses the potential adaptive value of differences in learning performance under the real conditions in which animals operate. This represents a first step towards filling a fundamental knowledge gap regarding how cognitive ability is tuned to the environment. The positive correlation between colony learning speed and foraging performance suggests there is strong directional selection for higher learning speed in bumblebees. Our results show that the slowest learning colonies brought in 40% less nectar than the fastest learning colonies.

However, as correlation does not necessarily indicate a causal relationship, we must consider alternative explanations for the observed pattern. Potentially a spurious correlation could be produced between colony learning speed and foraging performance, if both these factors were correlated with a third variable. Body size could be one such variable, because previous studies indicate that larger bumblebees are both more effective nectar foragers (Spaethe & Weidenmüller 2002; Ings *et al.* 2005) and have more sensitive eyes with greater visual acuity (Spaethe & Chittka 2003). However, although we found significant variation in worker body size (using both thorax width and body mass as indicators of body size) across the twelve colonies, we observed no significant correlation between body size and either learning speed or foraging performance in this study. The correlation between colony learning and foraging performance remained significant when the potential effects of intercolony variation in body size on both of these variables were removed by partial correlation. Parasitism represents another potential factor which could affect our correlation, as parasite infections appear to influence the foraging behaviour of bumblebees (P. Schmid-Hempel & Schmid-Hempel 1990; R. Schmid-Hempel & Müller 1991; P. Schmid-Hempel & Stauffer 1998) and may also affect their ability learn new associations (Mallon *et al.* 2003). Due to stringent precautions taken by commercial bee breeders to exclude parasites from their cultures (K Bolckmans, Koppert Biological Systems, pers. comm.), it is unlikely that our colonies were infected with parasites during the laboratory learning tests. This view is supported by our data, because the level of intercolony variation in learning speed among these 12 colonies is comparable to that shown by 16 colonies raised from wild caught queens screened for gut parasites (Raine *et al.* 2006b). Once colonies were taken into the field to measure foraging performance they might have been exposed to infection from parasites in the natural environment. However, whilst colonies might differ in their susceptibility to parasite infections in the same environment (P. Schmid-Hempel *et al.* 1999; Brown *et al.* 2000), exposure after completion of learning trials means that any differences in levels of infection among colonies could only affect foraging (not learning) performance in our study. Recent results also suggest that variation among colonies in innate colour preference (for violet over blue) can affect foraging performance (Raine & Chittka 2007a). In our previous study, we tested the colour preferences and foraging performance of colonies raised from wild caught queens in their natal habitat in which violet flowers produced considerably more nectar than blue flowers (Raine & Chittka 2007a). These results suggest innate colour preferences of resident colonies are adapted to local floral rewards. However, in this study we measured the foraging performance of commercially bred colonies, originally derived from a

population native to the eastern Mediterranean, in a flora to which they had never previously been exposed. It therefore seems unlikely that these colonies would possess specific sensory traits to enhance foraging in this local environment.

Support for inferring a causative link between variation in learning speed and colony foraging success would be strengthened if we could demonstrate that colonies varied in some other behavioural trait (not involving learning) which did not correlate with either learning or foraging performance. In this study, we found significant variation among colonies in the number of workers recorded foraging from the bicoloured flowers during pre-training in the laboratory (one-way ANOVA: $F_{11, 75} = 9.615$, $p < 0.005$), with the most active colonies sending out more than four times as many foragers as the least active colonies (means ± 1 SEM = 16.83 ± 2.54 versus 3.75 ± 0.77 foragers/ day). Interestingly, there was no correlation between this variation in propensity to send out foragers (under laboratory conditions) with either colony learning speed (t value: Pearson's correlation: $r = -0.200$, $p = 0.533$) or nectar foraging performance under natural conditions (Pearson's correlation: $r = 0.225$, $p = 0.483$). This finding suggests that overall levels of learning and/ or foraging performance cannot simply be explained by variation among colonies in behavioural state, therefore providing further evidence to support the inference of causation between variation in learning speed and colony foraging performance.

As bees forage in a complex and dynamic pollination market in which floral rewards differ strongly among plant species and vary over time (Heinrich 1979; Willmer & Stone 2004; Raine *et al.* 2006a), individual foragers must assess such differences, and respond accordingly (Chittka 1998; Menzel 2001; Chittka *et al.* 2003; Raine & Chittka 2007b). Rapid learning of salient floral cues, such as colour, presumably assists bees to track the changes in the floral rewards on offer, thereby improving bee foraging efficiency by allowing them to preferentially visit the current most profitable flower type (Raine *et al.* 2006a, b). It would be interesting to examine whether colonies which learn faster in visual tasks (e.g. learning colour associations) also show better learning performance in other modalities (e.g. odour or tactile cue learning). Laboratory studies (using the proboscis extension response paradigm) suggest that individual honeybees which are more sensitive to sucrose stimuli show improved learning in both odour and tactile conditioning experiments (Scheiner *et al.* 2001a, b). These results suggest that performance levels in an associative learning task using one modality might indeed be indicative of relative performance for other modalities, but this question deserves further direct investigation (ideally comparing learning performance using free flying bees).

To date, discussion of the potential adaptive value of learning has concentrated on the environmental conditions under which the learning (as opposed to no learning) will be favoured (Johnston 1982; Shettleworth 1998). However, these studies do not yet allow us to assess how the more subtle variation that exists between individuals in natural populations translates into fitness benefits. Some form of learning is predicted to be favoured in most environments, except those which are either so changeable that prior experience has no predictive value, or so consistent (across generations) that genetically pre-programmed innate behaviours alone are sufficient (Johnston 1982; Shettleworth 1998; Dukas 2004). Although simplistic this (presence/ absence of learning) framework appears sound because most animals demonstrate an ability to learn and operate in environments which change, but do not change so rapidly that the predictive value of forming associations become futile. The correlative approach we use here is a first step towards examining the fitness effects attributable to variation in learning performance under the real conditions to which animals are adapted. However, although our results suggest that variation in learning performance among bumblebee colonies represents the most likely explanation for observed differences in their foraging performance, we need further evidence to establish a causal link. In future it might be possible to selectively modify learning phenotypes, using double-stranded RNA interference (dsRNAi: Fire *et al.* 1998) or by creating more traditional knock-out mutants (Raine *et al.* 2006a), and compare the foraging performance of wild type and modified learning phenotypes. The choice of study organism for such an approach is a trade off between availability of techniques and the tractability of the organism for fitness studies under natural conditions. Whilst modifying the learning phenotype of fruit flies (*Drosophila* spp.) is more realistic in the short term, bumblebees could be used to test effects of such modified learning phenotype under more natural foraging conditions. Ultimately, in order to develop a more general understanding of the adaptive value of learning we must directly examine the fitness effects of variation in learning performance across a range of animal species and the environments to which they and their learning performance are adapted.

Acknowledgements: We thank Zainab Afzal, Denise Barrow, Samiya Batul, Rosa Hardt, Amanda Hill, Sibel Ihsan, Anna Lo, Nicole Milligan, Oscar Ramos Rodríguez, Miriam Sharp Pierson, Ralph Stelzer and Matthew Wallace for help with data collection, and Alice Raine for comments on the manuscript. This work was supported by the NERC (NER/A/S/2003/00469).

REFERENCES

- Brown, M. J. F., Loosli, R. & Schmid-Hempel, P. 2000. Condition dependent expression of virulence in a trypanosome infecting bumblebees. *Oikos* **91**, 421-427. (doi:10.1034/j.1600-0706.2000.910302.x)
- Capaldi, E. A. & Dyer, F. C. 1999. The role of orientation flights on homing performance in honeybees. *J Exp Biol* **202**, 1655–1666.
- Chittka, L. 1998. Sensorimotor learning in bumblebees: long-term retention and reversal training. *J Exp Biol* **201**, 515-524.
- Chittka, L., Dyer, A. G., Bock, F. & Dornhaus, A. 2003. Bees trade off foraging speed for accuracy. *Nature* **424**, 388. (doi:10.1038/424388a)
- Chittka, L., Ings, T. C. & Raine, N. E. 2004. Chance and adaptation in the evolution of island bumblebee behaviour. *Popul Ecol* **46**, 243-251. (doi:10.1007/s10144-004-0180-1)
- Chittka, L. & Raine, N. E. 2006. Recognition of flowers by pollinators. *Curr Opin Plant Biol* **9**, 428-435. (doi:10.1016/j.pbi.2006.05.002)
- Dukas, R. 1998. *Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making*. Chicago: University of Chicago Press.
- Dukas, R. 2004. Evolutionary biology of animal cognition. *Annu Rev Ecol Evol S* **35**, 347-374. (doi:10.1146/annurev.ecolsys.35.112202.130152)
- Dukas, R. & Bernays, E. A. 2000. Learning improves growth rate in grasshoppers. *Pro Natl Acad Sci USA* **97**, 2637-40. (doi:10.1073/pnas.050461497)
- Dukas, R. & Duan, J. J. 2000. Fitness consequences of associative learning in a parasitoid wasp. *Behav Ecol* **11**, 536-43. (doi:10.1093/beheco/11.5.536)
- Dukas, R. & Real, L. A. 1991. Learning foraging tasks by bees - a comparison between social and solitary species. *Anim Behav* **42**, 269-276. (doi:10.1016/S0003-3472(05)80558-5)
- Fire, A., Xu, S., Montgomery, M. K., Kostas, S. K., Driver, S. E. & Mello, C. C. 1998. Potent and specific genetic interference by double-stranded RNA in *Caenorhabditis elegans*. *Nature* **391**, 806-811. (doi:10.1038/35888)
- Gallistel, C. R. 1990. *The Organization of Learning*. Cambridge: MIT Press.
- Healy, S. D., de Kort, S. R. & Clayton, N. S. 2005. The hippocampus, spatial memory and food hoarding: a puzzle revisited. *Trends Ecol Evol* **20**, 17-22. (doi:10.1016/j.tree.2004.10.006)
- Heinrich, B. 1979. *Bumblebee Economics*. Cambridge/ USA: Harvard University Press.
- Ings, T. C., Schikora, J. & Chittka, L. 2005. Bumblebees, humble pollinators or assiduous invaders? A population comparison of foraging performance in *Bombus terrestris*. *Oecologia* **144**, 508-516. (doi:10.1007/s00442-005-0081-9)
- Ings, T. C., Ward, N. L. & Chittka, L. 2006. Can commercially imported bumblebees out-compete their native conspecifics? *J Appl Ecol* **43**, 940-948. (doi:10.1111/j.1365-2664.2006.01199.x)
- Johnston, T. D. 1982. Selective costs and benefits in the evolution of learning. *Adv Stud Behav* **12**, 65-106.

- Lunau, K., Wacht, S. & Chittka, L. 1996. Colour choices of naïve bumble bees and their implications for colour perception. *J Comp Physiol A* **178**, 477-489. (doi:10.1007/BF00190178)
- Mallon, E. B., Brockmann, A. & Schmid-Hempel, P. 2003. Immune response inhibits associative learning in insects. *Proc R Soc Lond B* **270**, 2471-2473. (doi:10.1098/rspb.2003.2456)
- Menzel, R. 1985. Learning in honey bees in an ecological and behavioral context. In *Experimental Behavioral Ecology* (eds. B. Hölldobler & M. Lindauer), pp. 55-74. Stuttgart, Gustav Fischer Verlag.
- Menzel, R. 2001. Behavioral and neural mechanisms of learning and memory as determinants of flower constancy. In *Cognitive Ecology of Pollination* (eds. L. Chittka & J. D. Thomson), pp. 21-40. New York, Cambridge University Press.
- Mery, F. & Kawecki, T. J. 2003. A fitness cost of learning ability in *Drosophila melanogaster*. *Proc R Soc Lond B* **270**, 2465-2469. (doi:10.1098/rspb.2003.2548)
- Mery, F. & Kawecki, T. J. 2004. An operating cost of learning in *Drosophila melanogaster*. *Anim Behav* **68**, 589-598. (doi:10.1016/j.anbehav.2003.12.005)
- Mery, F. & Kawecki, T. J. 2005. A cost of long-term memory in *Drosophila*. *Science* **308**, 1148. (doi:10.1126/science.11113331)
- Papaj, D. R. & Prokopy, R. J. 1989. Ecological and evolutionary aspects of learning in phytophagous insects. *Ann Rev Entomol* **34**, 315-350. (doi:10.1146/annurev.en.34.010189.001531)
- Raine, N. E. & Chittka, L. 2007a. Adaptive significance of sensory bias in a foraging context: floral colour preferences in the bumblebee *Bombus terrestris*. *PLoS One* **2**, e556. (doi:10.1371/journal.pone.0000556)
- Raine, N. E. & Chittka, L. 2007b. Pollen foraging: learning a complex motor skill by bumblebees (*Bombus terrestris*). *Naturwissenschaften* **94**, 459-464. (doi:10.1007/s00114-006-0184-0)
- Raine, N. E., Ings, T. C., Dornhaus, A., Saleh, N. & Chittka, L. 2006a. Adaptation, genetic drift, pleiotropy, and history in the evolution of bee foraging behavior. *Adv Stud Behav* **36**, 305-354. (doi:10.1016/S0065-3454(06)36007-X)
- Raine, N. E., Ings, T. C., Ramos-Rodríguez, O. & Chittka, L. 2006b. Intercolony variation in learning performance of a wild British bumblebee population (Hymenoptera: Apidae: *Bombus terrestris audax*). *Entomol Gen* **28**, 241-256.
- Scheiner, R., Page, R. E. & Erber, J. 2001a. The effects of genotype, foraging role, and sucrose responsiveness on the tactile learning performance of honey bees (*Apis mellifera* L.). *Neurobiol Learn Mem* **76**, 138-150. (doi:10.1006/nlme.2000.3996)
- Scheiner, R., Page, R. E. & Erber, J. 2001b. Responsiveness to sucrose affects tactile and olfactory learning in preforaging honey bees of two genetic strains. *Behav Brain Res* **120**, 67-73. (doi:10.1016/S0166-4328(00)00359-4)
- Schmid-Hempel, P., Pühr, K., Kruger, N., Reber, C. & Schmid-Hempel, R. 1999. Dynamic and genetic consequences of variation in horizontal transmission for a microparasitic infection. *Evolution* **53**, 426-434.

- Schmid-Hempel, P. & Schmid-Hempel, R. 1990. Endoparasitic larvae of conopid flies alter pollination behaviour of bumblebees. *Naturwissenschaften* **27**, 50-52. (doi:10.1007/BF01135951)
- Schmid-Hempel, P. & Stauffer, H.-P. 1998. Parasites and flower choice of bumblebees. *Anim Behav* **55**, 819-825. (doi:10.1006/anbe.1997.0661)
- Schmid-Hempel, R. & Müller, C. B. 1991. Do parasitized bumblebees forage for their colony? *Anim Behav* **41**, 910-912. (doi:10.1016/S0003-3472(05)80362-8)
- Sherry, D. F. & Healy, S. 1998. Neural mechanisms of spatial representation. In *Spatial Representations in Animals* (eds. S. Healy), pp. 133-158. Oxford, Oxford University Press.
- Shettleworth, S. J. 1998. *Cognition, Evolution, and Behavior*. Oxford: Oxford University Press.
- Spaethe, J. & Chittka, L. 2003. Interindividual variation of eye optics and single object resolution in bumblebees. *J Exp Biol* **206**, 3447-3453.
- Spaethe, J. & Weidenmüller, A. 2002. Size variation and foraging rate in bumblebees (*Bombus terrestris*). *Insectes Soc* **49**, 142-146. (doi:10.1007/s00040-002-8293-z)
- Willmer, P. G. & Stone, G. N. 2004. Behavioral, ecological, and physiological determinants of the activity patterns of bees. *Adv Stud Behav* **34**, 347-466.

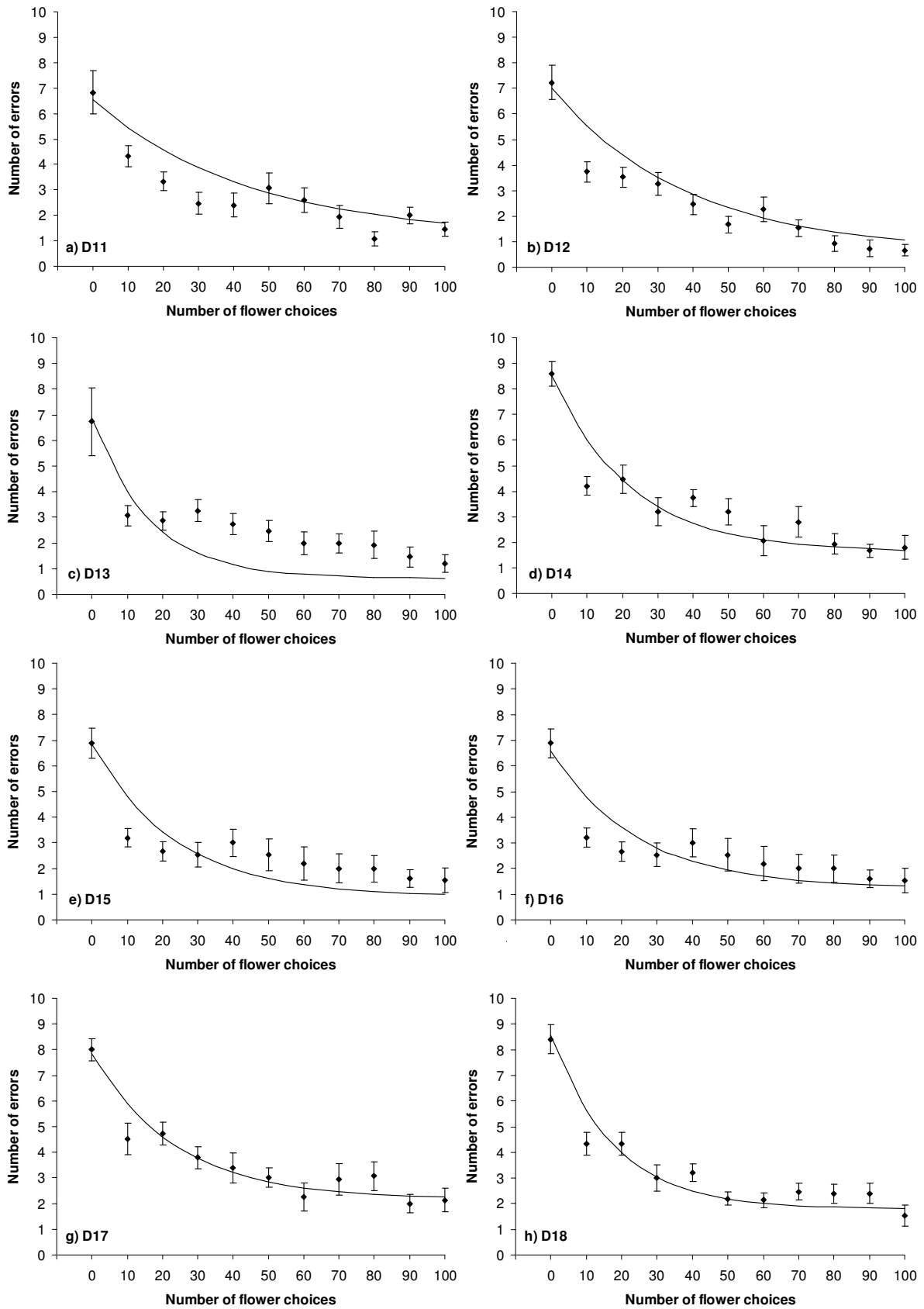
Figure legends

Figure 1. Average learning performance shown by individual bees from the 12 test colonies. In each panel (a-l) we present the mean learning performance averaged across bees tested in each colony (D11-D22). Data points (filled diamonds) represent the mean (± 1 SE) number of errors made during each consecutive group of flower choices. The starting point (i.e. number of flower choices = 0) was calculated from all bees which made at least five choices before feeding from (probing) a yellow (rewarding) flower for the first time. Subsequent data points each represent the mean number of errors (blue flowers chosen) during a series of 10 flower choices averaged across 12-15 bees per colony. All bees ($n = 172$) performed at least 100 flower choices. The curves shown in each figure panel indicate the mean learning curve for each colony. The colony learning curve is based on the mean curve parameters (y_0 , A and t) produced from fitting exponential decay functions ($y = y_0 + Ae^{-x/t}$) to the flower choice data for each individual bee and averaging parameter values across bees.

Figure 2. Learning speed of bumblebee (*B. terrestris*) colonies. These curves illustrate how improvement in task performance over time relates to the learning speed, expressed as the decay constant (t) in the equation: $y = y_0 + Ae^{-x/t}$. The curves shown present the mean learning speeds for the fastest (D19: $t = 9.25$, black line), an intermediate speed (D17: $t = 24$, grey line) and the slowest (D11: $t = 44.07$, pale grey line) learning colonies. All curves have amplitude (A) = 10, and saturation performance (y_0) = 0. Dashed lines indicate the average number of flower choices made by bees from each colony before achieving an 80% improvement in task performance.

Figure 3. Correlation between learning speed and nectar foraging performance for 12 bumblebee colonies. High t values correspond to slow learning, while low values are generated by fast learners. Data presented are colony mean values (-1 SEM) for both t value and foraging performance. On average colonies with higher learning speeds (lower t values) brought in more nectar per unit time (Pearson's correlation: $r = -0.588$, $n = 12$, $p = 0.044$).

Figure 1.



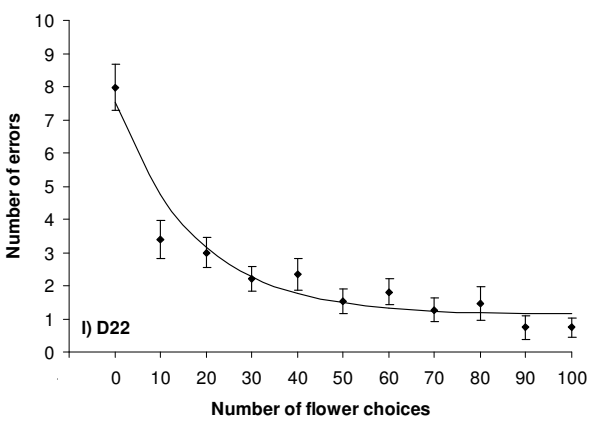
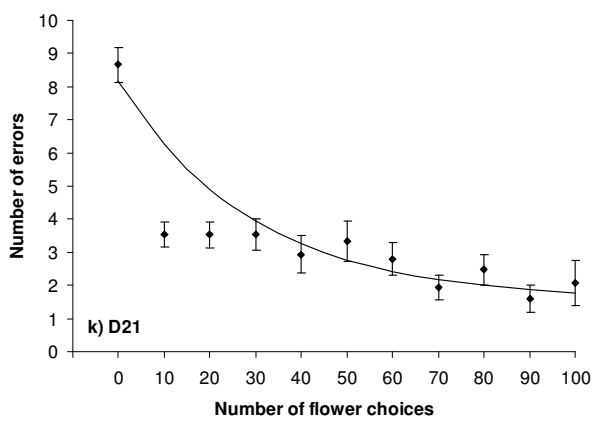
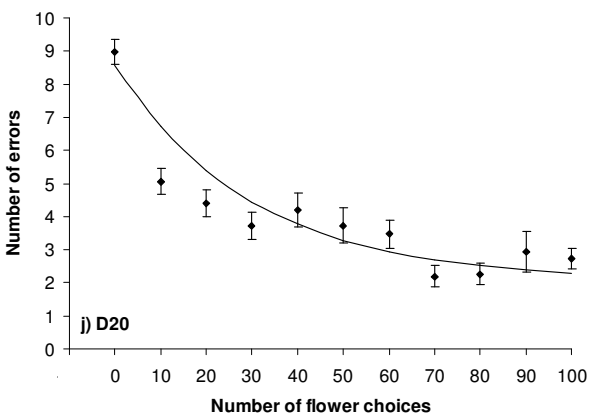
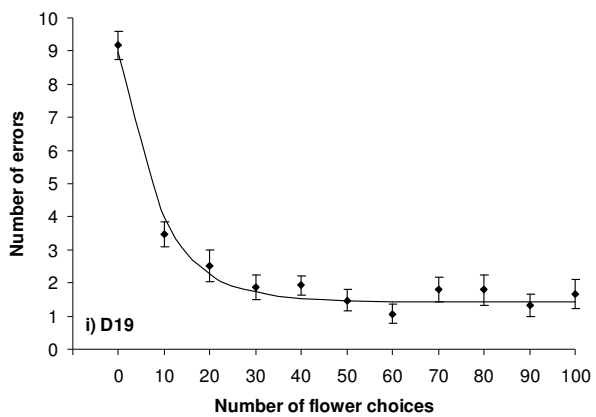


Figure 2.

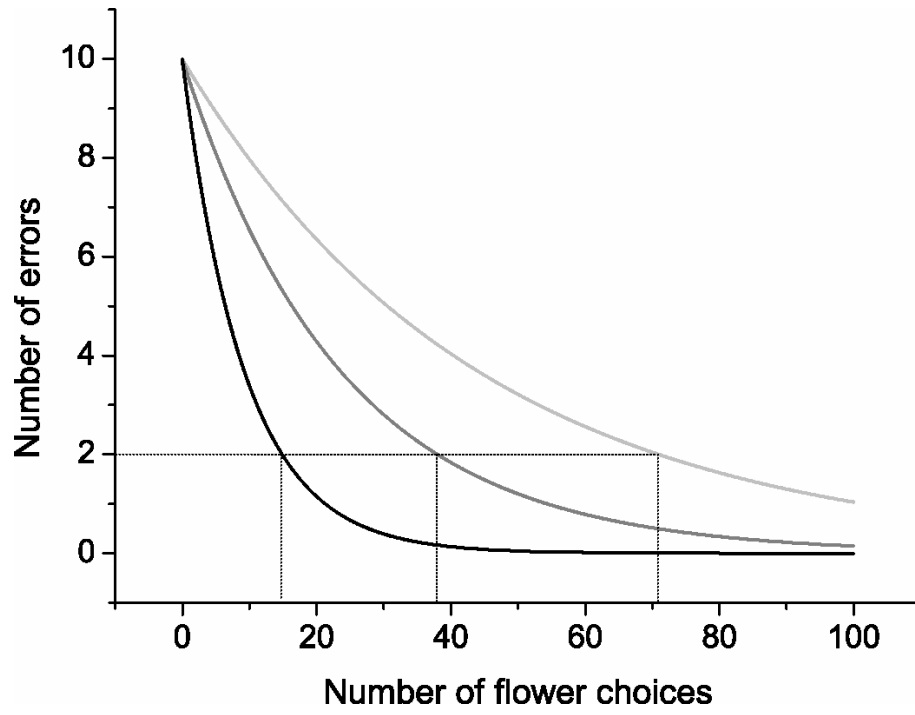


Figure 3.

