Behavioural Processes 167 (2019) 103918

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Interindividual variation in learning ability in honeybees

Catherine Tait, Aja Mattise-Lorenzen, Amanda Lark, Dhruba Naug*

Department of Biology, Colorado State University, Fort Collins, CO 80523, USA

ARTICLE INFO

Keywords:
Cognition
Landmark learning
Olfactory learning
Maneuverability
Survival
Honeybee

ABSTRACT

Performance on different cognitive tasks could either be positively correlated in an individual as a measure of general intelligence or costs related to specific aspects of cognition could give rise to specialized cognitive phenotypes. Social living offers the potential for individual specialization in learning and a cooperative group can benefit from a diversity of learning phenotypes. However, there is little empirical data regarding the nature of such interindividual variation in learning abilities in honeybees, a classic model of animal cognition. We tested for the presence of variation in learning abilities in the honeybee, *Apis mellifera*, and whether any component of learning has an influence on wing damage, a proxy for performance and survival. Our results show considerable interindividual variation in different types of learning abilities. At the individual level, while landmark and olfactory learning abilities are negatively correlated, olfactory learning shows a positive association with maneuverability performance, a measure which in turn shows a positive influence on wing damage, a proxy for survival. We discuss our results in the context of cognitive diversity and specialization in a social group.

1. Introduction

Cognition is central to questions about functional explanations of behavior as it outlines the various mechanisms by which individuals acquire, process, store and act on information from the environment (Shettleworth, 2009). Nonetheless, the ecological forces that contribute to the evolution of specific cognitive abilities remain poorly understood. In humans, performance on different cognitive tasks tends to be strongly positively correlated, a phenomenon described as "general intelligence" or "*g*" (Thornton and Lukas, 2012). However, demonstrations of this in other animals are relatively rare and ecological theories of cognition instead posit selection for specific cognitive domains and resulting tradeoffs among them in response to different environmental challenges (Shettleworth, 2009). Any such trade-offs are however often difficult to verify because studies traditionally focused on interspecific comparisons of cognitive capacity are generally confounded by various other factors. This has led to a recent surge of interest in intraspecific variation in cognitive ability with the expectation that it might offer better insights into the evolution of cognitive ability and its impact on fitness (Thornton et al., 2014; Cauchoix et al., 2018).

It has been proposed that interindividual cognitive differences within a species can translate to alternative behavioral strategies with different fitness consequences (Sih and Del Giudice, 2012). This suggests that such interindividual differences in cognitive abilities are especially likely to be fostered in group living species due to forces related to either competition or mutual benefit. Social insect colonies are prime examples of cooperative group living in which interindividual variation and the resulting adaptive diversity with respect to various traits is considered to be the major underlying force for their ecological success (Oster and Wilson, 1978; Jeanson and Weidenmüller, 2014). However, the patterns of such variation with respect to cognitive traits are less clear (Burns and Dyer, 2004; Raine et al., 2006; Muller and Chittka, 2012; Smith and Raine, 2014; Klein et al., 2017). Learning, the ability to adjust behavior through experience, is often considered to be fundamental to all cognitive mechanisms because it allows animals to adaptively respond to environmental contingencies (Dickinson, 2012; Heyes, 2012). In honeybees, one of the classic models of animal cognition, a large body of work has demonstrated how learning relates to cognition and how a variety of learning abilities is crucial to their performance (Menzel, 2012; Giurfa, 2015). However, there is little empirical data regarding if there is interindividual variation in these abilities and if any, whether it has any influence on performance.

In spite of the intuitive and obvious relevance of learning on performance and fitness, actual empirical demonstrations of a positive relationship between them have been relatively rare (Dukas, 1999; Cole et al., 2012; Maille and Schradin, 2016). In honeybees and other social insects, the performance of individuals is generally measured in terms of their work capacity, most commonly in terms of foraging. The extent

* Corresponding author.
E-mail address: dhruba@colostate.edu (D. Naug).

https://doi.org/10.1016/j.beproc.2019.103918
Received 18 November 2018; Received in revised form 23 July 2019; Accepted 23 July 2019
Available online 24 July 2019

of foraging activity performed by an individual is known to be reflected in the amount of wing damage, which results from collisions with foliage incurred during foraging (Foster and Cartar, 2011) and has a strong negative impact on survival and lifespan (Cartar, 1992). We therefore measured the amount of wing damage seen in an individual to test a relationship between learning and forager performance. The study comprises of a set of three experiments to examine interindividual differences in different learning abilities that are critical to foraging in honeybees and the relationship between learning ability and wing damage, which as a measure of individual forager survival acts as a proxy for fitness at the colony level.

2. Methods

2.1. Experiment 1

Bees from five colonies were trained to a setup for assaying the landmark learning ability of individuals. The subjects evaluated for their landmark learning were collected at the end of this assay and subjected to an olfactory learning assay.

2.1.1. Landmark learning assay

The assay consisted of a maze, configured from an array of acrylic boxes with white, opaque walls and clear tops and placed on a platform 50 m from the hives, which the bees had to negotiate in order to reach a reward of 30% sucrose solution (Zhang et al., 1996). There were two types of boxes that constituted the maze, decision and non-decision boxes (Supplement, Fig. S1). Decision boxes had three holes (4 cm diameter), each at the center of a different wall; a bee flew into such a box through one of these holes and it had to choose between the other two holes, one of which led into the next box in the correct path to the reward and the other which led to a dead end. Non-decision boxes had two holes and only required the bee to fly through one and exit through the other into the next box. The holes leading through the correct path in both decision and non-decision boxes were marked with a piece of blue tape to provide landmark cues. We used two different maze configurations during the experiment, 22 bees negotiated a maze with two decision boxes and 31 bees negotiated one with three.

Training consisted of placing a feeder filled with 30% sugar solution inside the first decision box and leaving it for 45 min to allow the bees to learn the landmark cue to enter the box. After 45 min, the feeder was moved into the second decision box in the path and so on for each decision box until the bees had learned the correct path through the maze to reach the reward placed in the final box. Bees were allowed to enter the maze freely, but were released from the top after acquiring the reward. Only bees that learned the entire path through the maze to the reward and were therefore foraging during the final 45 min of the training phase were individually marked and participated in the following test. The number of training trials each individual experienced during this time varied between 5 and 7, but was not controlled for.

Testing took place immediately after training. During the test, only one bee at a time was allowed to enter the maze to ensure that decisions were independent to each individual. A landmark learning score was assigned for each run through the maze to quantify its performance such that a score of 1 meant that the bee did not complete the maze within a maximum assigned time of five minutes, a score of 2 meant that the bee made one or more wrong turns, a score of 3 meant that the bee retraced its path but did not make any wrong turns, and a score of 4 meant that the bee negotiated the entire maze without making any mistakes. After a bee was tested on the maze thrice, it was collected for the olfactory learning assay.

2.1.2. Olfactory learning assay

Each bee was fed to satiation with a 30% sucrose solution and then starved for 18 h at 27 °C inside an incubator to increase their motivation for appetitive learning. Each bee was then tested for its olfactory learning ability using the Proboscis Extension Reflex (PER) assay (Bitterman et al., 1983). The assay consisted of presenting an individual bee with an odor (Conditioned Stimulus or CS) followed by a sucrose reward (Unconditioned Stimulus or US) in 6 consecutive trials with an inter trial interval of 11 min and recording the extension of the proboscis by the bee for the reward. A bee was considered to have learned the association between the CS and the US and was given a score of 1 in a trial if it showed a conditioned response (CR) by extending its proboscis to the odor prior to the sucrose reward being provided. If the bee did not extend its proboscis at all or extended it only at the presentation of the sucrose reward, it was given a score of 0 in that trial. The total number of CRs for a bee was defined as its olfactory learning score.

2.2. Experiment 2

Brood frames were collected from two colonies just before adult emergence and kept in an incubator maintained at 32 °C. Newly emerged adults were marked with a distinct color on their thorax and returned to the colony. These marked bees were collected when they were at least two weeks old as they left the hive on foraging flights and subjected to the following assays.

2.2.1. Maneuverability assay

The assay consisted of placing an individual bee in a flight arena (an acrylic box measuring 41.5 × 26.5 × 17 cm) containing an array of obstacles comprised of wooden pegs stuck to the floor of the box (Mountcastle et al., 2016). The walls of the box were covered with a floral pattern and the box was placed under an overhead white light to stimulate flight. The box was placed on an orbital shaker rotating at 3 rpm to simulate the moving obstacles in the foliage that a bee might naturally encounter while foraging. Each subject was allowed to fly in the arena for five minutes and its behavior was recorded using a digital video camera (Sony HDV 1080i). The flight behavior of a bee was analyzed in terms of two parameters: (a) number of landings, defined as the events when a bee settled on a peg or the floor, its feet touching first, and (b) number of collisions, defined as the events when the bee hit a peg, a wall, or the ceiling and could not maintain flight elevation and crashed to the floor. Following successful completion of the flight assay, individuals were subjected to the PER assay as described in the first experiment.

2.3. Experiment 3

Newly emerged bees from two source colonies were marked and fostered in the colony, following which they were collected from the entrance of the colony as described above. These bees were subjected to the maneuverability assay as described above and following it each subject was euthanized and its wings were collected and analyzed for existing damage in the following manner. The two forewings were removed at the wing joint, their images were scanned into the computer and the area and perimeter of each wing was measured using ImageJ software (Foster and Cartar, 2011).

2.4. Data analysis

As we were specifically interested in the relationship between different learning abilities and their relationship with performance, we only included learners or bees with an olfactory learning score ≥ 1 in our data analysis for the first two experiments. In Experiment 1, there was no significant difference in the landmark learning score between bees in the two maze types ($F_{1, 51} = 0.01$, $P = 0.91$), so data from the two were pooled. In Experiments 2 and 3, the maneuverability performance of a bee was measured by calculating the ratio of the number of landings to that of crashes (landings/crashes), where a higher value represents a higher performance. In Experiment 2, the relationship between maneuverability performance and olfactory learning was examined by using a linear mixed model with colony of origin and age of the bee as random effects and the significance of random effects were tested using likelihood ratio tests. In Experiment 3, wing damage of a bee was determined by calculating the ratio of perimeter to area (perimeter/area) and then averaging that measure across the two wings, where a larger value represents a higher damage. Due to the relatively small number of bees for each specific age, bees were divided into two discrete age groups: young bees (12–17 days) and old bees (20–24 days) and a linear mixed model was used to examine the influence of maneuverability and age on wing damage with colony of origin as a random effect. While some of the data showed a better fit with non-linear models, we chose linear models for biological parsimony. All statistical analyses were performed in R version 3.4.1.

3. Results

There was significant interindividual variation observed in the different learning abilities assayed in each experiment. The distribution of the scores for each assay was significantly different from a normal distribution (Shapiro-Wilk test, Landmark learning: $W = 0.48$, $P < 0.001$; Olfactory learning: $W = 0.9$, $P < 0.001$; Maneuverability: $W = 0.94$, $P = 0.02$, Fig. 1).

In Experiment 1, there was a significant negative association between the landmark and olfactory learning performance of an individual bee (Pearson's Correlation; $r = -0.17$, $N = 31$, $P = 0.01$; Fig. 2).

In Experiment 2, there was a significant positive association between olfactory learning and maneuverability performance ($F_{1,36} = 4.81$, $P < 0.001$, Fig. 3). There were no significant effects of either source colony or age (Colony: $\chi^2 < 0.001$, $P = 0.9$; Age: $\chi^2 = 1.98$, $P = 0.15$) on this relationship.

In Experiment 3, maneuverability performance of an individual had a significant independent effect on the observed damage on its wings ($F_{1,31} = 5.10$, $P = 0.03$; Fig. 3), such that bees with higher maneuverability showed less wing damage (Fig. 4). While age did not have a significant independent effect on wing damage ($F_{1,31} = 2.18$, $P = 0.15$), it showed a significant interactive effect with maneuverability to influence wing damage such that older and less agile bees showed more wing damage ($F_{1,31} = 5.57$, $P = 0.02$). There was also a significant effect of colony of origin on the observed wing damage ($\chi^2 = 4.83$, $P = 0.02$).

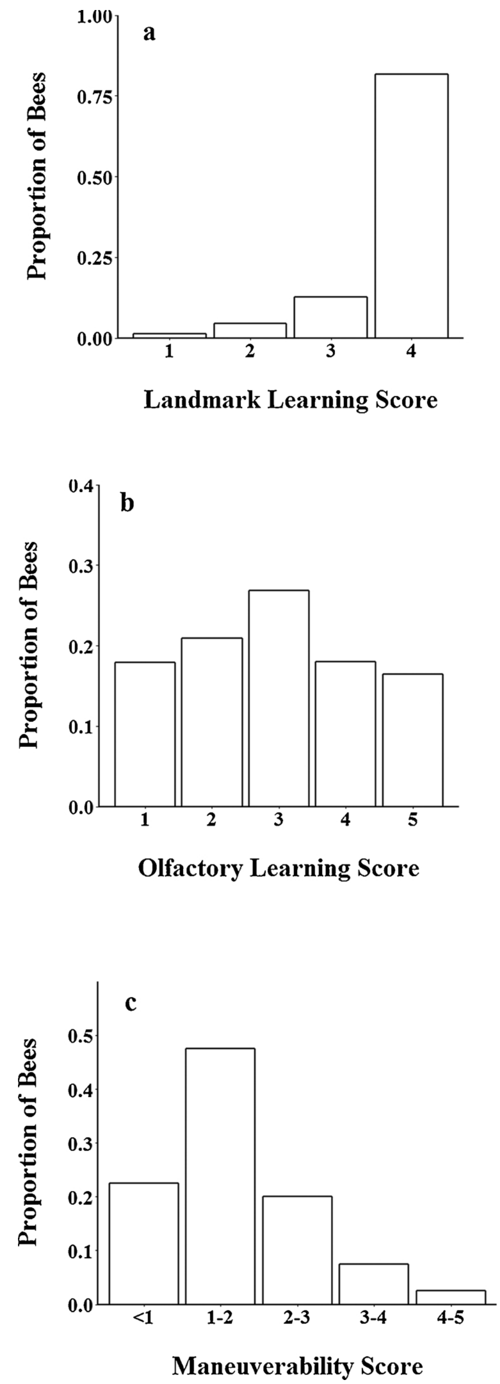

Fig. 1. Frequency distributions of a) landmark learning, b) olfactory learning, and c) maneuverability scores observed across all bees in the different experiments.

4. Discussion

Our results show that there are significant differences among honeybee individuals in terms of their performance across the three tasks such that most individuals have high landmark learning ability while individuals seem more variable in terms of olfactory learning and maneuverabilithy. This suggests landmark learning may be a more general cognitive skill that is common to all foragers while relatively fewer foragers in the colony exhibit enhanced olfactory learning or maneuverability skills that may be required for more specialized foraging tasks. There is evidence to suggest that scouts, a relative minority in the colony, perform better on olfactory learning tasks compared to recruits (Carr-Markell and Robinson, 2014; Cook et al., 2019). It is possible that the diversity of performance on different learning tasks may reflect distributions of such different behavioral phenotypes within the colony. The different aspects of learning that are crucial to foraging performance show both positive and negative correlations among them in an individual bee. Our first experiment demonstrated a negative association between landmark and olfactory learning while our second experiment demonstrated a positive association between maneuverability and olfactory learning. While it might be tempting to consider the positive association as evidence for the "g" factor, one should note that our maneuverability assay, requiring bees to avoid obstacles in flight and therefore also consisting of a motor component, is not purely a learning task.

While the notion of cognitive specialization is generally based on poor and good performers on a single learning task (Carr-Markell and Robinson, 2014; Cook et al., 2019), to the best of our knowledge this is the first time a specialization based on a negative correlation between the performance in two different types of learning tasks has been demonstrated in individual honeybees. This observed negative association between two types of learning in individuals has important implications for division of labor in social insect colonies, the models for which generally require individuals showing negative correlations between their response to different stimuli (Beshers and Fewell, 2001). Since previous findings documenting positive correlations between learning

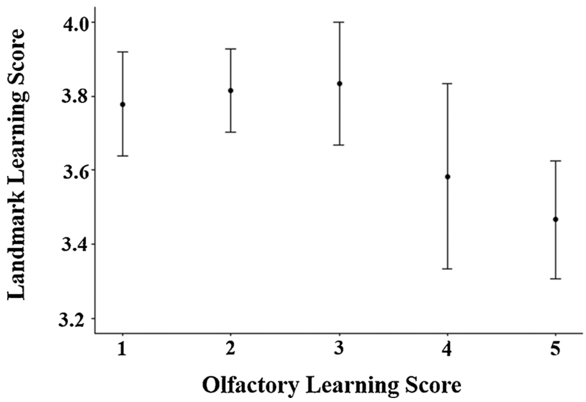

Fig. 2. Correlation between landmark and olfactory learning performance of individual bees (N = 31) with data representing mean ± standard error across bees.

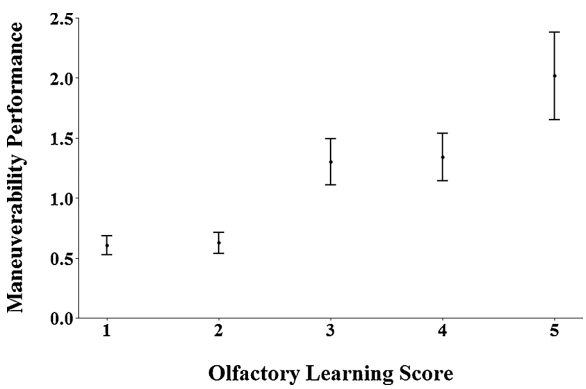

Fig. 3. Relationship between olfactory learning and maneuverability with data representing mean ± standard error across bees (N = 37).

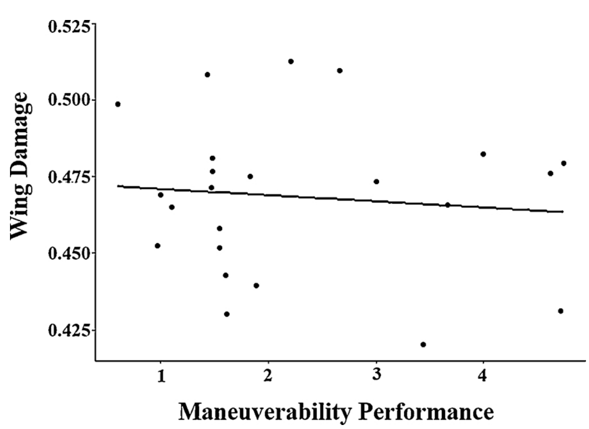

Fig. 4. Average wing damage in individual bees (N = 34) as a function of their maneuverability score. Each point represents an individual bee and the solid line represents the regression (y = –0.007x + 0.47) between maneuverability and wing damage.

performance across different sensory modalities and sucrose responsiveness (Page et al., 2006) are somewhat at odds with such models, our results demonstrating a negative correlation between certain types of learning provide support regarding how individuals might show different proficiencies in performing different tasks. The observed negative correlation between performance in these learning tasks, despite the positive correlation seen between them and sucrose sensitivity, therefore also suggests that it is not likely an outcome of differences at the sensory level but rather due to a difference at a higher cognitive level.

Our findings support the idea that investment costs related to learning (Mery and Kawecki, 2004, 2005; Jaumann et al., 2013) may necessitate a tradeoff between performance in different learning modalities, leading to individual specialization. The fact that such learning specialization has not been observed in bumblebees (Muller and Chittka, 2012; Smith and Raine, 2014) may have to do with their lower degree of sociality compared to honeybees. The relationship between behavioral specialization and colony size or sociality has long been debated and there is evidence supporting the idea that larger and more eusocial colonies tend to have more specialized workers (Amador-Vargas et al., 2015; Kamhi et al., 2016). Studies also show that an increase in social complexity is accompanied by an increase in the capacity for distributed cognition mediated by more social communication and specialized brains (Lihoreau et al., 2012; O'Donnell et al., 2015). In smaller or less social groups such as bumblebees, individuals may need to maintain capacity in a broader range of learning modalities to allow them to be successful generalists while large honeybee colonies through specialization can profit from maintaining a cognitively diverse workforce.

Our results showing a positive relationship between olfactory learning and maneuverability and the influence of the latter on wing wear also for the first time suggest a possible consequence of inter-individual variation in learning ability on performance in honeybees. It has been well established that in flying insects such as honeybees, wing damage has several functional consequences that include increased mortality resulting from factors such as increased vulnerability to extrinsic elements and increased energy expenditure (Cartar, 1992; Burkhard et al., 2002; Higginson and Barnard, 2004; Combes et al., 2010; Dukas and Dukas, 2011). A significant contributor to wing damage is the number of collisions bees encounter with vegetation while foraging (Foster and Cartar, 2011), which means that individuals with higher maneuverability, by better avoiding collisions, should gain in terms of survival and their foraging lifespan. While maneuverability is likely a product of both cognitive and motor skills and our experimental design is unable to distinguish between the two, it nevertheless underlines the point that variation in learning ability, by influencing individual foraging performance and lifespan, can have a significant influence on colony performance. While wing damage must initially arise from poor maneuverability, it is likely that maneuverability and wing damage exhibit a positive feedback loop, whereby a decreased maneuverability leads to further wing damage.

It is interesting to ask if there is any selection at the colony level to maintain interindividual variation and individual specialization in different learning modalities in large social groups such as the honeybee colony. If differences in learning ability correlate to different social roles, a colony may benefit from maintaining learning specialization and cognitive diversity (Burns and Dyer, 2004). For example, the two behavioral phenotypes among honeybee foragers, dancers that gather information and followers that use that information, may require different types of cognitive skills. Our earlier work has shown dancers and followers to be functionally equivalent to producers and scroungers, respectively (Katz and Naug, 2016), behavioral phenotypes that are known to be driven by differences in their learning ability (Katsnelson et al., 2011). Our future research directions therefore include examining if different behavioral phenotypes in a honeybee colony correlate to distinct cognitive phenotypes and if colonies with different distributions of these phenotypes show colony level differences in performance.

Acknowledgements

This study was partly supported by a NSF CAREER award to DN. DN and CT designed the experiments and wrote the manuscript; CT analyzed the data; CT collected the data for experiments 2 and 3, AM-L and AL collected the data for experiment 1.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2019.103918.

References

Amador-Vargas, S., Gronenberg, W., Wcislo, W.T., Mueller, U., 2015. Specialization and group size: brain and behavioural correlates of colony size in ants lacking morphological castes. Proceedings of the Royal Society B: Biological Sciences 282, 20142502.

Beshers, S., Fewell, J., 2001. Models of division of labor in social insects. Annu. Rev. Entomol. 46, 413–430.

Bitterman, M.E., Menzel, R., Fietz, A., Schäfer, S., 1983. Classical conditioning of proboscis extension in honeybees (*Apis mellifera*). J. Comp. Psychol. 97, 107–119.

Burkhard, D., Ward, P., Blanckenhorn, W., 2002. Using age grading by wing injuries to estimate size-dependent adult survivorship in the field: a case study of the yellow dung fly Scathophaga stercoraria. Ecol. Entomol. 27, 514–520.

Burns, J.G., Dyer, A.G., 2004. Diversity of speed-accuracy strategies benefits social insects. Curr. Biol. 18, 953–954.

Carr-Markell, M.K., Robinson, G.E., 2014. Comparing reversal-learning abilities, sucrose responsiveness, and foraging experience between scout and non-scout honey bee (*Apis mellifera*) foragers. J. Insect Behav. 27, 736–752.

Cartar, R.V., 1992. Morphological senescence and longevity: an experiment relating wing wear and life span in foraging wild bumble bees. J. Anim. Ecol. 61, 225–231.

Cauchoix, M., Chow, P.K.Y., van Horik, J.O., Atance, C.M., Barbeau, E.J., Barragan-Jason, G., Bize, P., Boussard, A., Buechel, S.D., Cabirol, A., Cauchard, L., Claidière, N., Dalesman, S., Devaud, J.M., Didic, M., Doligez, B., Fagot, J., Fichtel, C., Henke-von der Malsburg, J., Hermer, E., Huber, L., Huebner, F., Kappeler, P.M., Klein, S., Langbein, J., Langley, E.J.G., Lea, S.E.G., Lihoreau, M., Lovlie, H., Matzel, L.D., Nakagawa, S., Nawroth, C., Oesterwind, S., Sauce, B., Smith, E.A., Sorato, E., Tebbich, S., Wallis, L.J., Whiteside, M.A., Wilkinson, A., Chaine, A.S., Morand-Ferron, J., 2018. The repeatability of cognitive performance: a meta-analysis. Philos. Trans. Biol. Sci. 373, 20170281.

Cole, E.F., Morand-Ferron, J., Hinks, A.E., Quinn, J.L., 2012. Cognitive ability influences reproductive life history variation in the wild. Curr. Biol. 22, 1808–1812.

Combes, S.A., Crall, J.D., Mukherjee, S., 2010. Dynamics of animal movement in an ecological context: dragonfly wing damage reduces flight performance and predation success. Biol. Lett. 6, 426–429.

Cook, C.N., Mosqueiro, T., Brent, C.S., Ozturk, C., Gadau, J., Pinter-Wollman, N., Smith, B.H., 2019. Individual differences in learning and biogenic amine levels influence the division between foraging honeybee scouts and recruits. J. Anim. Ecol. 88, 236–246.

Dickinson, A., 2012. Associative learning and animal cognition. Philos. Trans. Biol. Sci. 367, 2733–2742.

Dukas, R., 1999. Cost of memory: ideas and predictions. J. Theor. Biol. 197, 41–50.

Dukas, R., Dukas, L., 2011. Coping with nonrepairable body damage: effects of wing damage on foraging performance in bees. Anim. Behav. 81, 635–638.

Foster, D.J., Cartar, R.V., 2011. What causes wing wear in foraging bumble bees? J. Exp. Biol. 214, 1896–1901.

Giurfa, M., 2015. Learning and cognition in insects. Wiley Interdiscip. Rev. Cogn. Sci. 6, 383–395.

Heyes, C., 2012. Simple minds: a qualified defence of associative learning. Philos. Trans. R. Soc. Lond. B Biol. Sci. 367, 2695–2703.

Higginson, A.D., Barnard, C.J., 2004. Accumulating wing damage affects foraging decisions in honeybees (*Apis mellifera L.*). Ecol. Entomol. 29, 52–59.

Jaumann, S., Scudelari, R., Naug, D., 2013. Energetic cost of learning and memory can cause cognitive impairment in honeybees. Biol. Lett. 9, 20130149.

Jeanson, R., Weidenmuller, A., 2014. Interindividual variability in social insects - proximate causes and ultimate consequences. Biol. Rev. 89, 671–687.

Kamhi, J.F., Gronenberg, W., Robson, S.K.A., Traniello, J.F.A., 2016. Social complexity influences brain investment and neural operation costs in ants. Proceedings of the Royal Society B: Biological Sciences 283, 20161949.

Katsnelson, E., Motro, U., Feldman, M.W., Lotem, A., 2011. Individual-learning ability predicts social-foraging strategy in house sparrows. Proceedings of the Royal Society B: Biological Sciences 278, 582–589.

Katz, K., Naug, D., 2016. Dancers and followers in a honeybee colony differently prioritize individual and colony nutritional needs. Anim. Behav. 119, 69–74.

Klein, S., Pasquaretta, C., Barron, A.B., Devaud, J.-M., Lihoreau, M., 2017. Inter-individual variability in the foraging behaviour of traplining bumblebees. Sci. Rep. 7, 4561.

Lihoreau, M., Latty, T., Chittka, L., 2012. An exploration of the social brain hypothesis in insects. Front. Physiol. 3, 1–7.

Maille, A., Schradin, C., 2016. Survival is linked with reaction time and spatial memory in African striped mice. Biol. Lett. 12, 20160346.

Menzel, R., 2012. The honeybee as a model for understanding the basis of cognition. Nat. Rev. Neurosci. 13, 758–768.

Mery, F., Kawecki, T., 2004. An operating cost of learning in Drosophila melanogaster. Anim. Behav. 68, 589–598.

Mery, F., Kawecki, T.J., 2005. A cost of long term memory in Drosophila. Science 208, 1148.

Mountcastle, A.M., Alexander, T.M., Switzer, C.M., Combes, S.A., 2016. Wing wear reduces bumblebee flight performance in a dynamic obstacle course. Biol. Lett. 12, 20160294.

Muller, H., Chittka, L., 2012. Consistent interindividual differences in discrimination performance by bumblebees in colour, shape and odour learning tasks (*Hymenoptera: apidea: bombus terrestris*). Entomol. Gen. 34, 1–8.

Page, R., Scheiner, R., Joachim, E., Amdam, G., Schatten, G., 2006. The development and evolution of division of labor and foraging specialization in a social insect (*Apis mellifera*). Curr. Top. Dev. Biol. 74, 253–286.

O'Donnell, S., Bulova, S.J., DeLeon, S., Khodak, P., Miller, S., Sulger, E., 2015. Distributed cognition and social brains: reductions in mushroom body investment accompanied the origins of sociality in wasps (Hymenoptera: Vespidae). Proceedings of the Royal Society B: Biological Sciences 282, 20150791.

Oster, G.F., Wilson, E.O., 1978. Caste and Ecology in the Social Insects. Princeton University Press, Princeton.

Raine, N.E., Ings, T.C., Ramos-Rodriguez, O., Chittka, L., 2006. Intercolony variation in learning performance of a wild British bumblebee population (Hymenoptera: apidae: *bombus terrestris audax*). Entomol. Gen. 28, 241–256.

Shettleworth, S., 2009. Cognition, Evolution and Behavior. Oxford University Press, New York.

Sih, A., Del Giudice, M., 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. Philos. Trans. Biol. Sci. 367, 2762–2772.

Smith, K.E., Raine, N.E., 2014. A comparison of visual and olfactory learning performance in the bumblebee, Bombus terrestris. Behav. Ecol. Sociobiol. (Print) 68, 1549–1559.

Thornton, A., Lukas, D., 2012. Individual variation in cognitive performance: developmental and evolutionary perspectives. Philosop. Trans. R. Soc. B: Biol. Sci. 367, 2773–2783.

Thornton, A., Isden, J., Madden, J.R., 2014. Toward wild psychometrics: linking individual cognitive differences to fitness. Behav. Ecol. 25, 1299–1301.

Zhang, S.W., Bartsch, K., Srinivasan, M.V., 1996. Maze learning by honeybees. Neurobiol. Learn. Mem. 66, 267–282.