



Nesting ecology does not explain slow–fast cognitive differences among honeybee species

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Abstract

Slow–fast behavioral and life history differences have been tied to slow–fast variation in cognition that is part of the general speed-accuracy tradeoff. While there is growing evidence for such cognitive variation and its association with behavior and life history at the intraspecific level, it is unknown if a similar relationship extends to the interspecific level. Since interspecific differences in cognition have been shown to be a function of ecology and life history, such differences should be reflected in multiple traits that comprise the slow–fast cognitive axis. In this study, by measuring multiple cognitive traits in individuals, we tested for differences in the cognitive phenotype among four honeybee species, which differ in their behavior and life history in a manner that is associated with differences in their nesting ecology. Our results indicate that a set of cognitive traits consistently covary within each species, resulting in slow and fast cognitive phenotypes that largely meet the predictions of the speed-accuracy tradeoff. We also find that the four species group into two distinct clusters on a slow–fast cognitive axis, although their positions do not align with the known differences in their life history and nesting ecology. We instead find that cognitive differences among the four species are correlated with their brain size. We discuss the possible implications of these results for the role of ecology on slow–fast cognitive differences and the evolution of cognition.

Keywords Cognition · Cognitive variation · Cognitive phenotype · Slow–fast interspecific differences · Honeybees

Introduction

The evolution of cognitive variation and how it determines differences in behavior is a question of fundamental interest in animal behavior (Dukas 2004; Thornton and Lukas 2012; Griffin et al. 2015; Morand-Ferron and Quinn 2015; Boogert et al. 2018). There is strong evidence that cognitive traits can evolve as a function of differences in ecology and life history and factors such as the complexity of the physical environment, social structure, diet and mating behavior have been identified as possible explanations for cognitive differences among species (Macphail and Bolhuis 2001; Bolhuis 2005; Healy et al. 2009; Chittka et al. 2012; Cauchoux and Chaine 2016). Although comparative studies have greatly enhanced our understanding of the ecological

factors that drive variation in cognition, these studies are generally limited to looking at variation in a single cognitive trait—learning ability. This focus on a single trait limits our understanding regarding how ecological differences might drive variation in the overall cognitive phenotype, which is comprised of multiple other cognitive traits such as risk sensitivity, neophilia, sampling tendency, impulsivity, etc. (Sih and Del Giudice 2012). It has, therefore, been suggested that measuring how multiple cognitive traits covary to influence behaviors may provide a more complete understanding of the link between cognitive and behavioral variability (Griffin et al. 2015). While some recent studies have used this approach at the intraspecific level (Keagy et al. 2009; Mazza et al. 2018; Tait and Naug 2020), measuring such covariation patterns across related species is key to understanding how differences in ecology can shape cognitive differences.

Both intra- and interspecific differences regarding a variety of phenotypic traits have recently been described with a theoretical framework known as the Pace-Of-Life Syndrome, in which individuals are placed along a slow–fast axis, each end of which is associated with a specific suite of physiological, behavioral, and life history traits (Réale et al. 2010). It

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has also been proposed that this slow–fast pace-of-life axis is aligned with a slow–fast cognitive axis described by the speed–accuracy tradeoff, which predicts fast individuals to show higher levels of learning, risk, sampling, neophilia and impulsivity, leading them to make more rapid but somewhat more inaccurate decisions, compared to slow individuals (Sih and Del Giudice 2012). There is indeed some recent evidence at the intraspecific level that links slow–fast differences in behavior and life history with cognitive differences that correspond to slow and fast cognitive phenotypes (Amy et al. 2012; Tait and Naug 2020). However, it has never been tested whether a slow–fast cognitive axis comprising multiple cognitive traits is consistent across related species and if interspecific differences in cognitive traits are similarly distributed along a slow–fast gradient or they occupy unique positions that match similar differences in their behavior and life history (Fig. 1). Interspecific comparisons of cognitive traits using such an approach can help shed light on the role of ecological factors in driving the evolution of slow–fast cognitive phenotypes.

Honeybees as a taxonomic group are an attractive prospect for such studies of comparative cognition due to the well-established status of *Apis mellifera* as a model with a rich cognitive repertoire that can be rigorously measured under both laboratory and field conditions (Menzel 2012). The existence of interindividual cognitive variation is well-documented in *A. mellifera* (Smith and Raine 2014; Tait et al. 2019), variation that is also known to have a significant influence on foraging performance and other life history traits (Page et al. 2006; Tait and Naug 2020). However, our extensive knowledge regarding such cognitive variation in honeybees is largely derived from *A. mellifera*, with little known about cognitive traits in other honeybee species such as *A. cerana*, *A. florea* and *A. dorsata* (but see Kaspi and Shafir, 2013; Wang and Tan 2014). There are significant ecological differences among the four honeybee species that is largely related to differences in their nesting behavior

(Seeley 1982). Previous comparative work has suggested that the selection pressure to maintain a larger worker population for protection in the open nesting species, *A. dorsata* and *A. florea*, has resulted in workers with a longer lifespan that is associated with a slower behavioral and life history “tempo” than those in the cavity nesting species, *A. cerana* and *A. mellifera* (Dyer and Seeley 1991; Bhagavan et al. 2016; Bhagavan and Brockmann 2019). It has recently been shown that several behavioral and life history traits covary with cognitive traits to define slow–fast phenotypes within *A. mellifera* (Mugel and Naug 2020; Tait and Naug 2020). In this study, we test whether multiple cognitive traits similarly covary to define a consistent slow–fast cognitive axis and distinct cognitive phenotypes in all the four honeybee species and whether any cognitive differences among them are correlated with the known differences in their behavioral and life history tempo related to their nesting ecology. If slow–fast difference in life history and behavior are correlated with slow–fast differences in cognition, then based on the biology of the four species, *A. mellifera* and *A. cerana* are predicted to express a faster cognitive phenotype than *A. dorsata* and *A. florea*.

Methods

The cognitive assays with *Apis mellifera* were conducted with bees from colonies ($N=3$) maintained in Fort Collins, Colorado. Capped brood was extracted from a colony one day prior to adult emergence and kept overnight in an incubator set at 32 °C. Upon emergence, adults were paint marked and put in a queen-right observation hive. The assays with the three tropical honeybee species were conducted with their colonies (2 colonies of *A. cerana*, 3 colonies of *A. florea* and 1 colony of *A. dorsata*) maintained in the campus of the National Center for Biological Sciences in Bangalore, India. Due to the general propensity of *A. dorsata* for

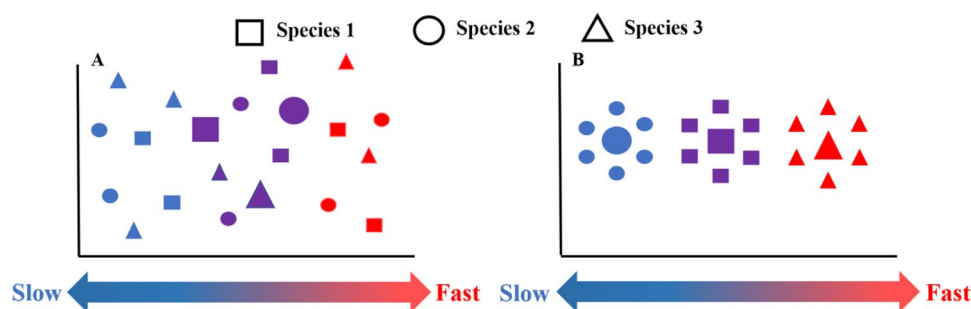


Fig. 1 Possible alternative models describing the position of individuals from three hypothetical species along a slow–fast cognitive axis described in a two-dimensional cognitive trait space, where small shapes represent individuals of each species and large shapes represent the respective species means. **a** Depicts a scenario where

individuals of each species are similarly distributed along the entire slow–fast cognitive axis while **b** depicts a scenario where individuals of each species occupy a unique position on the cognitive axis such that some species are relatively slow and some are relatively fast in terms of their cognitive phenotype

nesting in difficult, often remote, locations, it was possible to use one colony of this species. Additionally, due to the exceptional difficulty of extracting brood and introducing marked bees in the colonies of the three tropical nesting species, none of their foragers could be age marked, and we subsequently did not use age as a statistical variable in any of the four species. All bees used for the assays were collected at a sucrose feeder away from the colonies to ensure that they were foragers. They were immobilized on ice, harnessed within a plastic tube and fed to satiation with 30% sucrose solution and then starved for 24 h in an incubator set at 27 °C to increase their motivation for appetitive conditioning based on the Proboscis Extension Reflex (PER).

Cognitive assays

Associative learning

The associative learning ability of an individual bee was determined using the PER assay, which consists of presenting a bee with an odor (Conditioned Stimulus, CS) followed by a sucrose reward on its antennae (Unconditioned Stimulus, US) with a partial overlap between the two, in a series of trials (Bitterman et al. 1983). Our PER assay consisted of a 5 s CS pulse over a constant air stream and a US of 0.2 µl of 30% sucrose solution delivered by a Gilmont microsyringe 3 s after the onset of the CS, creating a 2-s overlap between the CS and the US. Each bee was presented with six such trials with a 5-min inter-trial interval (ITI), with hexanol, octanone, geraniol and linalool as the CS odors used in different replicates. A bee is considered to have learned the association between the CS and the US when it extends its proboscis (a Conditioned Response, CR) to the CS prior to the US delivery, and the total number of CR (excluding the response on the first trial since it cannot be classified as a CR) is used as a measure of its associative learning ability.

Sampling and preference for novelty

30 min following the associative learning assay, each bee was subjected to a forced-choice proboscis extension response assay to assess both sampling behavior and novelty preference (Shafir et al. 1999; Katz and Naug 2015; Tait and Naug 2020). This assay consists of presenting two different odors to the subject on opposite sides of its head, each odor being presented twice in two alternating 0.8-s nonoverlapping pulses with 0.2 s of odorless air in between successive odor pulses. Based on the orientation of its head and the extension of its proboscis at the end of the four odor pulses, a choice for one of the two odors is scored for the subject. Using the odor that was paired with the reward during the associative learning assay as one of the two odors and a novel odor as the other odor, preference for novelty

is recorded as a binary score (1 or 0) and the number of times an individual turned its head toward each odor during the entire sequence of the four odor pulses provides a measure of sampling (Katz and Naug 2015; Tait and Naug 2020). The pairing of each odor and the direction of odor presentation was balanced across experimental replicates to account for any possible odor and side biases. Following the sampling and novelty preference assay, bees were fed to satiation with 30% sucrose solution and maintained in a dark incubator set at 27 °C for 24 h.

Preference for variance (risk)

24 h after the novelty assay, a PER assay was used to train the bees to associate two different odors with two different reward distributions. This consisted of pairing one odor with a variable reward and another with a constant reward and presenting these pairings to each bee in a predetermined pseudorandom sequence in a series of 20 trials with an ITI of 5 min (Shafir et al. 1999; Mayack and Naug 2011; Tait and Naug 2020). In a trial in which the subject was presented with the odor that was paired with the variable reward, it received either a high reward of 0.4 µl of 30% sucrose or no reward (0 µl) in a predetermined pseudorandom sequence such that the overall probability of obtaining each reward type was 0.5. In a trial in which the subject was presented with the odor paired with the constant reward, it always received a 0.2 µl reward of 30% sucrose. Therefore, both the constant and the variable reward distribution had a mean of 0.2, but the variable one had a coefficient of variation (CV) of 100. The preference for variance for an individual was calculated as the number of times it extended its proboscis to the variable reward, divided by the total number of times it responded to the two rewards.

Statistical analysis

Since we were interested in the covariation across all the four cognitive traits, only those bees which completed all the four assays were used in the data analysis. Generalized linear models were first used to test for the effects of the different odors used and the direction of odor presentation wherever applicable (Table S1). Generalized linear models were then used to test for differences in each of the four cognitive traits across the four species. A principal component analysis (PCA) was then performed separately for each species to determine the covariance among the four different cognitive traits within each species and if such a covariance pattern could be used to define a cognitive axis (R package *stats*). All data were mean-centered and standardized for PCA analysis. Following the PCA, a cluster analysis was performed with squared Euclidean distances (k-means method) to group individuals of each species based on their

scores on the first principal component. A canonical variate analysis (CVA), which determines the association between multiple variables and can maximize the separation between a priori defined groups in a multivariate space, was then used to group the four species according to their performance on the four cognitive traits (R package Morpho). The first two canonical variate components for all the individuals were then represented as a bivariate scatterplot and the centroid for each species was calculated as a geometric mean of all the individuals of that species. While both PCA and CVA are similar techniques that are used in multivariate analysis to reduce the number of variables, CVA maximizes the variance explained between groups (in this case, species) while PCA maximizes the variance explained among individuals (Carter and Feeney 2012).

A multi-response permutation procedure (MRPP, R package vegan), a technique that calculates whether there is a difference between a priori defined groups (species here) was used to determine the extent of cognitive dissimilarity among the four species. Groups that are clustered in multidimensional space have lower average distances, δ , to their group centroid than their inter-group centroids and, therefore, are dissimilar to the other groups. To assess the fit of each individual to its group, the group membership of each individual was randomized in each permutation and the resulting δ values (δ_{exp}) were compared to the observed δ (δ_{obs}) to calculate a p value. Within group agreement, A , was calculated as $1 - (\delta_{\text{obs}})/(\delta_{\text{exp}})$ to measure how well the individuals fit within their respective groups. If A is 1, all individuals within each group are identical, and it is 0 if all individuals behave randomly. All analyses were performed in R version 3.4.1.

Results

Our results indicate the presence of significant variation in cognitive traits both within and between species. In general, *A. mellifera* and *A. dorsata* were more similar to each other and *A. cerana* and *A. florea* were more similar to each other across all the four cognitive traits. An analysis of variance (ANOVA) revealed significant differences in associative learning ($F_{3,127} = 10.6$, $p < 0.001$) and sampling frequency ($F_{3,127} = 7.53$, $p < 0.001$), but not in preference for novelty ($\chi^2_{3,127} = 5.54$, $p = 0.13$) or preference for risk ($F_{3,127} = 1.77$, $p = 0.15$) among the four species (Fig. 2).

Within each of the four species, the variance explained by the first two principal components was similar (Table 1). For the first principal component, on average, preference for novelty had the highest loading (0.56), followed by associative learning (0.48), sampling (0.43) and risk preference (0.38). The covariance structure among the different cognitive traits, defined by the positive or negative loadings that

described the first principal component, was also largely similar. A covariance structure defined by a positive covariance between preference for novelty and associative learning and their negative covariance with sampling was consistent in three of the four species except *A. dorsata* in which preference for novelty showed a negative covariance with associative learning. Across the four species, this covariance structure appeared well conserved, *A. mellifera* and *A. florea* had exactly the same covariance structure among the four traits, and three of the four traits also covaried similarly in *A. cerana* and *A. dorsata*. Due to the significantly lower amount of variance explained by it, we did not consider the covariance structure defined by the second principal component. The cluster analysis revealed two distinct clusters in each species (*A. mellifera*: Kruskal–Wallis rank sum test $\chi^2_{(1,36)} = 24.97$, $p < 0.001$; *A. cerana*: $\chi^2_{(1,17)} = 11.01$, $p < 0.001$; *A. dorsata*: $\chi^2_{(1,41)} = 29.15$, $p < 0.0001$; *A. florea*: $\chi^2_{(1,37)} = 26.84$, $p < 0.0001$), separated along the first principal component axis.

Among the four species, a large percentage of the variance was explained by the first canonical variate in which there was a positive covariance between preference for novelty and associative learning, both these showing a negative covariance with preference for risk (Table 2). Based on the loadings on the first canonical variate, the largest differences between the species are defined by their preference for risk and their associative learning ability, resulting in two distinct clusters of species, with one group comprised of *A. mellifera* and *A. dorsata* showing lower risk preference and higher associative learning compared to the other group composed of *A. florea* and *A. cerana* (Fig. 3a). The MRPP supported the presence of these two distinct groups of species that differed significantly in terms of their cognitive traits (MRPP: $A = 0.08$, observed $\delta = 3.97$, expected $\delta = 4.24$, $p < 0.01$, Fig. 3b).

Discussion

Our results indicate a largely similar suite of covarying cognitive traits in the four honeybee species. The slow–fast cognitive axis observed here is based on a positive covariation between associative learning ability, preference for novelty and risk and their negative covariance with sampling, which meets the predictions of a speed–accuracy tradeoff (Sih and Del Giudice 2012) and results in ‘slow’ and ‘fast’ cognitive phenotypes that were also previously seen in *A. mellifera* (Tait and Naug 2020). In this cognitive axis, high associative learning and high preference for novelty and risk define a ‘fast’ cognitive phenotype, while low associative learning and low preference for novelty and risk define a ‘slow’ cognitive phenotype (Sih and Del Giudice 2012). In our study, at least three of these four traits were always similarly

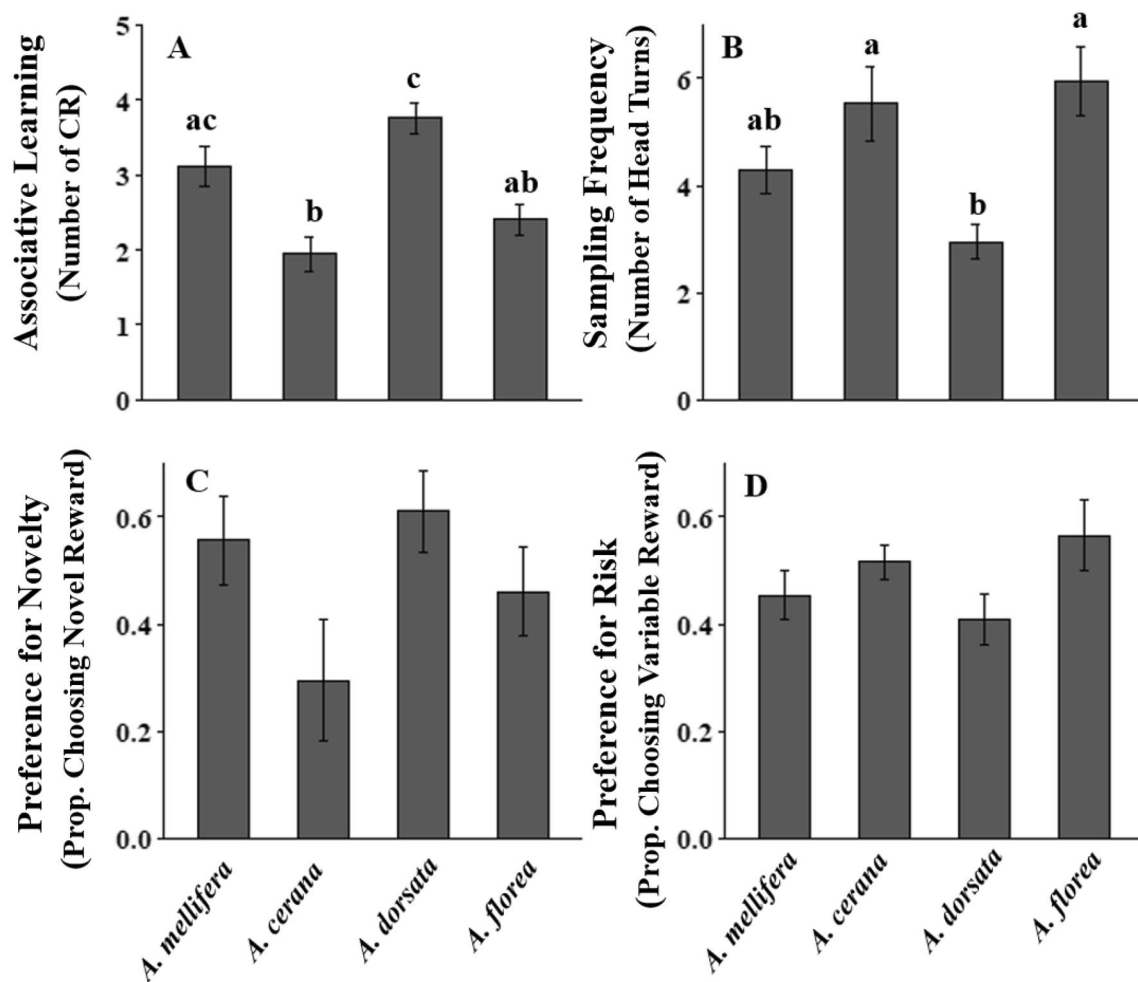


Fig. 2 **a–d** Cognitive differences among four honeybee species (*A. mellifera*: $N=36$, *A. cerana*: $N=17$, *A. dorsata*: $N=41$, *A. florea*: $N=37$) in terms of **a** associative learning, **b** sampling frequency, **c**

preference for novelty, and **d** preference for risk. Bars represent mean $\pm$ SE with significant differences shown with different letters. (Pos-hoc comparisons in Table S2)

Table 1 Principal components with eigenvalues ≈ 1 and their rotated component loadings, and the percentage of total variance explained for each species

Trait	<i>A. mellifera</i>		<i>A. cerana</i>		<i>A. dorsata</i>		<i>A. florea</i>	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Associative Learning	0.51	-0.17	0.57	-0.23	-0.21	-0.76	-0.63	0.37
Sampling	-0.27	0.88	-0.54	-0.37	-0.65	0.13	0.28	0.55
Preference for Novelty	0.55	0.38	0.35	-0.78	0.65	0.08	-0.69	0.06
Preference for Risk	0.59	0.20	-0.48	-0.42	0.32	0.62	-0.16	-0.74
Variance explained	0.48	0.24	0.46	0.25	0.49	0.27	0.36	0.27
Eigenvalue	1.95	0.97	1.84	1.01	1.67	1.08	1.45	1.10

Bold outlines depict the common covariance structure conserved across the four species

Table 2 The two canonical variates and their representative behaviors

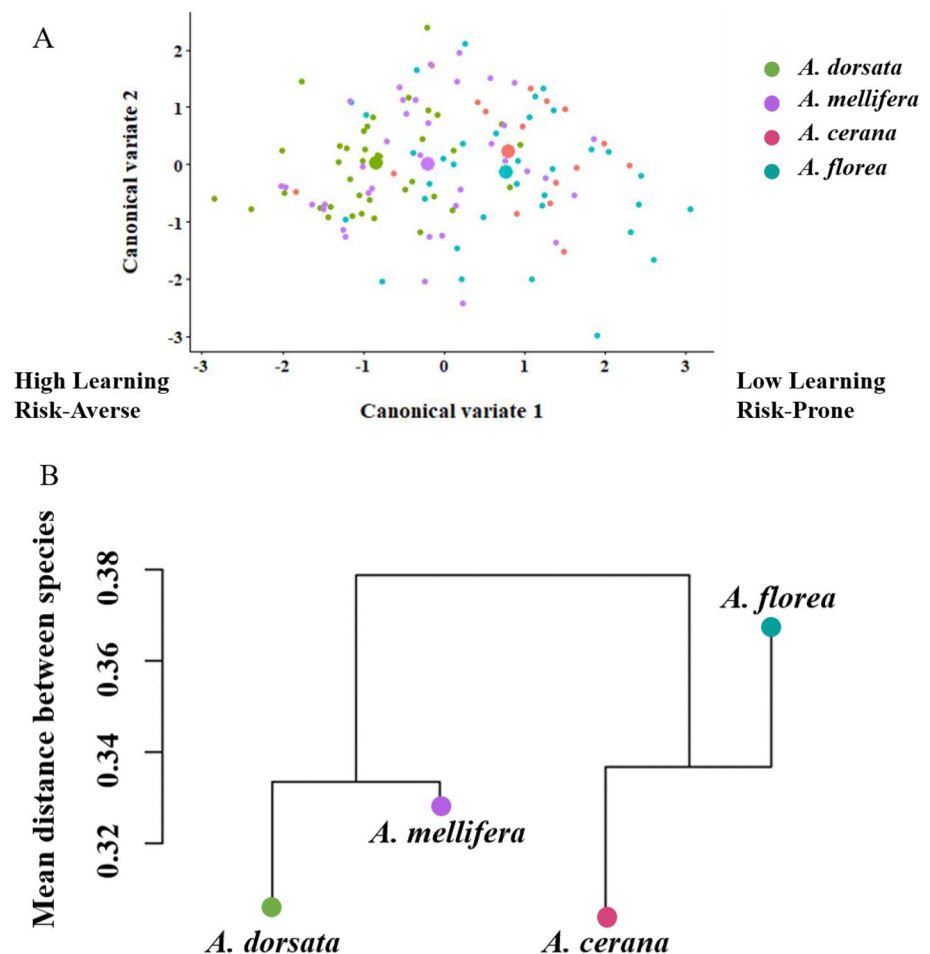
Cognitive trait	CV1	CV2
Associative learning	− 0.52	− 0.31
Sampling	0.19	− 0.21
Preference for novelty	− 0.23	− 1.26
Preference for risk	1.39	− 0.82
% Variance explained	0.95	0.04

correlated in each of the four species, showing remarkable consistency regarding this slow–fast cognitive axis across the different species. To the best of our knowledge, this is the first time that multiple cognitive traits have been measured in individuals of related species for a comparative study in the framework of a slow–fast cognitive axis. The repeated presence of fast and slow cognitive phenotypes defined by similar cognitive traits indicates a likely adaptive basis to this phenotypic diversity, the positive effects of which have been shown in a foraging context in honeybees (Dyer et al. 2014). At the colony level, this diversity is likely related to the functional equivalence between behavioral and cognitive

phenotypes in honeybees where, based on their overall difference in learning and preference for novelty and risk, scouts and recruits can be, respectively, seen to reflect the difference between fast and slow cognitive phenotypes (Tait and Naug 2020).

We also found evidence in support of a scenario in which the different honeybee species occupy unique positions on this cognitive axis such that some species are relatively slow and some are fast. However, it is interesting that the trait covariance structure at the within-species level was not fully consistent with the one at the between-species level and the largest difference separating them was their respective risk preference, and future research should closely examine the relationship between risk-preference and the ecology of these species. While our measure of risk is one based on economics and the preference for variability, it may be interesting to consider how cognitive mechanisms related to risk in this context may be related to behavioral mechanisms related to the sensitivity to predation risk. A possible link between the two may be mediated through the common currency of energetics, which has been proposed as the fundamental driver of all slow–fast differences (Biro and Stamps

Fig. 3 The position of the four honeybee species in a multivariate cognitive trait space defined by two canonical variates and represented as, **a** a bivariate plot where each smaller point represents an individual honeybee and the four larger points indicate the respective centroids for each species, and **b** a dendrogram using mean distances between species in the cognitive trait space, where horizontal lines indicate mean dissimilarity between species while length of termini indicate dissimilarity of a species within the cluster, with termini pointing upward indicating species that are more heterogeneous than the combined cluster



2008; Réale et al. 2010). The four species also did not align on the slow–fast cognitive axis as what would be predicted based on the known differences in behavior and life history among them, which are in turn correlated with their nesting ecologies.

Based on their longer worker lifespan and lower behavioral tempo, it has been suggested that the open nesting *A. dorsata* and *A. florea* are the two ‘slow’ species while the cavity nesting *A. mellifera* and *A. cerana* are the two ‘fast’ species (Dyer and Seeley 1991). Our results, however, indicate that it is *A. cerana* and *A. florea* which cluster together as a group with a significantly higher risk preference and lower learning performance than *A. mellifera* and *A. dorsata*. How does one explain this observed pattern of cognitive differences among the four species if they are not explained by a difference in their nesting ecology and thereby their associated differences in life history? One possibility is to consider other differences among them in terms of traits such as body size and metabolic rate that are typically considered to be important in driving slow–fast phenotypic differences (Biro and Stamps 2008; Réale et al. 2010). However, metabolic rate seems an unlikely explanation for the observed pattern because differences in metabolic rate are correlated along the same lines as nesting ecology with the two cavity nesting species showing higher mass-specific metabolic rate than the two open nesting species (Dyer and Seeley 1991).

In terms of body size, *A. dorsata* and *A. mellifera* are significantly larger than *A. cerana* and *A. florea* (Dyer and Seeley 1991) and related to the possible influence of these size differences, but one that is more pertinent to cognition, we found an interesting difference among the four species in terms of brain size that is correlated with the observed difference in their cognition. Using the data of Gowda and Gronenberg (2019), an analysis of the absolute brain volume of each species resulted in two distinct clusters where the two larger species have significantly larger brain size than the two smaller species (Kruskal Wallis rank sum test: $\chi^2_{1,31} = 22.51$, $p < 0.001$, Fig. 4). The two species with significantly larger brains, *A. mellifera* and *A. dorsata*, are the two species which are more risk-averse and show higher associative learning, compared to *A. cerana* and *A. florea*, which have smaller brains. While differences in brain size among the four species can be attributed to isometric scaling related to differences in their body size, some recent evidence suggests that absolute brain size may be a better predictor of performance on cognitive traits than brain size corrected for body mass, especially among closely related species (Deaner et al. 2007; Herculano-Houzel 2011; MacLean et al. 2014). While the relationship between brain size and all cognitive traits is not well-known, the positive relationship between brain size and learning ability has been widely reported (Reader and Laland 2002; Buechel et al. 2018). However, the relationship between cognitive phenotype and brain size

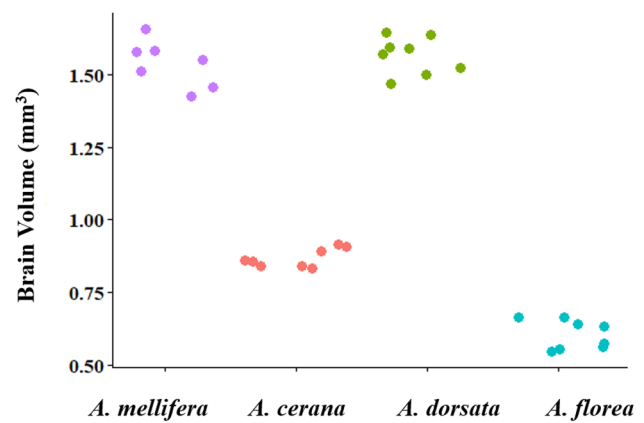


Fig. 4 Brain volume differences among the four honeybee species with points representing individuals (*A. mellifera*: $N=7$; *A. cerana*: $N=8$; *A. dorsata*: $N=8$; *A. florea*: $N=8$). Brain volume for each species was derived from the dataset of Gowda and Gronenberg (2019)

observed here needs to be interpreted with caution since the overall neural architecture or cell number that equate to the number of neurons in different brain regions may be a more important predictor of cognition in animals with small brains such as insects (Chittka and Niven 2009; Lihoreau et al. 2012).

In social insects, spatial learning and sensory ecology related to foraging are known to have played a significant role in the evolution of brain size and architecture (Farris 2016; Kamhi et al. 2016). In line with this hypothesis, there are large differences in foraging habit among the four honeybee species (Seeley 1982; Dyer and Seeley 1991). Of the two species with larger brains, *A. mellifera* inhabits a more ephemeral foraging environment while *A. dorsata* has a much larger foraging range relative to *A. cerana* and *A. florea*. Since the complexity of foraging environment has been shown to be correlated with increases in brain size (Roth and Pravosudov 2009; Roth et al. 2010), it is possible that similar forces have played a role in the observed differences in brain size and cognitive traits among the four honeybee species. The role of ecological factors such as foraging in complex spatiotemporal environments on the evolution of brain size is a major question in cognitive ecology (Sherry et al. 1992; Rosati 2017; Tello-Ramos et al. 2019) although we know little about such relationships in these various honeybee species, and it would be interesting to investigate how foraging ecology shapes the specific traits comprising the slow–fast cognitive axis. There is evidence in honeybees that increased foraging experience related to processing of both visual and olfactory information leads to an increase in the size of the mushroom bodies, the neural regions responsible for higher order cognitive processing (Durst et al. 1994).

In summary, our results demonstrate that different cognitive traits covary quite consistently in the four honeybee

species and largely meet the predictions of the speed-accuracy tradeoff. The specific covariance pattern among the different cognitive traits that result in slow-fast cognitive phenotypes within each species may reflect certain differences among the species that are broadly not correlated with known differences in their life history, behavior or nesting ecology. Although we could not make repeated measures on these cognitive traits due to the exceptional challenge of working with these bees, it would be useful to explore the consistency of such cognitive variation in the future, maybe working with a more limited number of traits at a time. While previous work suggests that the trait covariance patterns are largely consistent across colonies (Tait and Naug 2020), individual level differences such as foraging experience and colony level factors related to the nutritional and social environment should also be considered in future comparative studies, although it is likely to be a challenging task. The two open nesting species are migratory, often abandoning their nests to avoid inclement conditions and this potentially reduces the need to sequester large stores of honey compared to closed nesting species, which might result in individuals of the different species varying in their motivation for appetitive learning that defined the assays used in this study. Developing aversive learning assays to measure the same cognitive traits could be a potential solution to this issue. Future research should also try to explore a larger range of ecological factors that differ among these species and expand upon the number of species in a comparative approach to test if there are other more relevant factors that explain the observed cognitive differences among the different honeybee species.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10071-021-01515-2>.

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Author contributions DN and CT designed the study and wrote the manuscript, CT collected and analyzed the data and AB provided funding, logistical and infrastructure support for the research conducted in Bangalore, India.

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Declarations

Conflict of interest The authors declare no competing or financial interests.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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