




RESEARCH ARTICLE

Considering variation in bee responses to stressors can reveal potential for resilience

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Abstract

1. Environmental stressors frequently have sublethal consequences for animals, often affecting the mean of phenotypic traits in populations. However, effects on inter-individual variability are poorly understood. Since phenotypic variability is the basis for adaptation, any change due to stressors may have important implications for population resilience.
2. Here, we explored this possibility in bees by analysing raw datasets from 23 studies (5618 bees) in which individuals were first exposed to stressors and then tested for cognitive tasks.
3. While all types of stressors decreased the mean cognitive performance of bees, they increased cognitive variability. Focusing on 14 pesticide studies, we found that the mode of exposure to stressors and the dose were critical. Mean cognitive performance was more affected by a chronic exposure than by an acute exposure. Yet, cognitive variability increased with increasing doses following both exposure durations.
4. *Policy implications.* Current guidelines for the authorization of plant protection products on the European market prioritize acute over chronic toxicity assessments on non-target organisms. By overlooking the consequences of a chronic exposure, regulatory authorities may register new products or doses that are harmful to bee populations. Our findings call for more research on stress-induced phenotypic variation and its incorporation into policy guidelines to help identify levels and modes of exposure animals can cope with.

KEYWORDS

Apis cerana, *Apis mellifera*, *Bombus impatiens*, *Bombus terrestris*, cognition, inter-individual variability, pesticides, pollinators

Amélie Cabirol, Tamara Gómez-Moracho and Coline Monchanin contributed equally to the work.

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1 | INTRODUCTION

Human activities have led to a dramatic increase in the extinction rates of animal species (Barnosky et al., 2011; Dirzo et al., 2014; Wagner, 2020). Anthropogenic stressors have partly been identified and act synergistically (Brook et al., 2008; Sánchez-Bayo & Wyckhuys, 2019). These include climate change, habitat loss, various types of pollution, and the introduction of invasive species. These factors add up to the ones naturally encountered by animals in their environment, such as the presence of predators, pathogens, and parasites. Given the raising number of species threatened with extinction (Barnosky et al., 2011; Sánchez-Bayo & Wyckhuys, 2019), it has become urgent to understand how animal populations can cope with human-induced stressors to orient policies towards a more efficient regulation of activities affecting the biodiversity.

Many of these stressors do not kill animals, but, nevertheless, significantly impact their fitness through inaccurate behaviour or reduced reproduction (Klein et al., 2017). Measuring the sublethal effects of stressors on populations is difficult because of the need to monitor large numbers of animals and tease apart the many confounding factors linked to field conditions. Most studies have thus focused on the effects of stressors on individual animals using controlled laboratory setups to measure single phenotypic traits, such as activity, cognition or reproduction (Badyaev, 2005). Yet, the relevance of such risk assessment methods compared with field population-level studies has been questioned as mismatching conclusions often emerged from the two approaches (Henry et al., 2015; Thompson & Maus, 2007). Even though stressors may affect individual phenotypic traits in the laboratory, life in a natural, sensory and socially enriched environment can buffer or amplify these effects (Cabirol et al., 2017; Henry et al., 2015; Lambert et al., 2016; Wright & Conrad, 2008).

Studies investigating the impact of stressors on phenotypic traits often report shifts in their means at the population level. Agrochemicals, for instance, were shown to reduce food consumption and delay migration in songbirds (Eng et al., 2019), to alter endocrine functions in amphibians and fish (Besson et al., 2020; Mann et al., 2009), and to reduce learning performance in bees (Siviter et al., 2018). We argue that studying how stressors affect the variability of these traits among individuals will provide important complementary information about the severity of stressors on animal populations. Indeed, it is well recognized that animals exhibit variability in behavioural and physiological responses to stressors (Ebner & Singewald, 2017; Mazza et al., 2019). Some individuals may better cope with stressors than others. Thus understanding how this variability in stress response is affected at the population level is crucial for risk assessment (Nakagawa et al., 2015). If the variability in the population becomes low following stressor exposure, all individuals may suffer the consequences associated with the altered phenotype. On the contrary, if the variability remains high in the population, even though the mean is affected, some individuals may still exhibit an adaptive phenotype. In some cases, stressors may even increase inter-individual phenotypic variability, a phenomenon

suggested promoting the evolutionary diversification of species (Badyaev, 2005). Stressors act as agents of selection and stress-induced variation should therefore be considered when assessing the resilience of a population to a particular stressor (Hoffmann & Merilä, 1999).

Here we highlight the importance of studying the phenotypic variability in animal populations exposed to stressors. We illustrate this approach by analysing the effect of stressors on the mean and inter-individual variability of cognitive performances in bees. We focused on managed bees, honey bees (*Apis*) and bumblebees (*Bombus*), as they are by far the most studied pollinators in behavioural and cognition research (Chittka, 2022; Goulson, 2010; von Frisch, 1955). They are also known to be affected by multiple natural and human-induced stressors, and in particular pesticides (Goulson et al., 2015; Potts et al., 2010; Vanbergen & Garratt, 2013). Honey bees and bumblebees live in colonies with a division of labour and are therefore characterized by an important level of inter-individual behavioural and cognitive variability (Jeanson & Weidenmüller, 2014). Foragers, in particular, have evolved a rich cognitive repertoire enabling them to locate and recognize plant resources, handle them, and navigate back to their hive to unload food for the colony (Chittka, 2017). One of the most reported sublethal effect of stressors on bees is the decrease in their cognitive performance (assessed through learning and memory), which has been associated with a decreased foraging success and colony survival (Gill et al., 2012; Klein et al., 2017). A recent meta-analysis confirmed that both acute and chronic exposures to neonicotinoid pesticides at field-realistic doses consistently alter the mean olfactory learning and memory performance of bees (Siviter et al., 2018). However, the impact of stressor intensity (dose and duration) on the inter-individual variability in learning performance was not analysed. We therefore explored these effects by analysing the raw datasets from 23 studies that assessed bee cognition applying olfactory and visual learning protocols in either an appetitive or aversive context. Although a decreased cognitive performance was expected in stressed bees, we predicted that the effect of stressors on the variability would depend on the stressor intensity, which would help estimate the hazardous nature of a given stressor.

2 | MATERIALS AND METHODS

2.1 | Search and selection of datasets

The search for datasets in scientific publications falling within the scope of our research question was performed in July 2020 using the PubMed database. The words used for the search were ('Stressor' OR 'Pesticide' OR 'Parasite') AND ('Cognition' OR 'Learning') AND ('Bees'). This search was not restricted to any section of the manuscripts and automatically extended to similar terms intended under the MeSH hierarchy of the database. A total of 240 studies were found, of which 18 met our inclusion criteria regarding the cognitive task and the type of stressor (see below).

TABLE 1 Summary of the 23 studies used.

Stressor	Bee genus	Exposure type	Reference
Pesticide	<i>Apis</i>	Acute	Ludicke and Nieh (2020)
Pesticide	<i>Apis</i>	Acute	Hesselbach and Scheiner (2018)
Pesticide	<i>Apis</i>	Acute	Urlacher et al. (2016)
Pesticide	<i>Apis</i>	Acute	Tan et al. (2015)
Pesticide	<i>Apis</i>	Chronic	Mustard et al. (2020)
Pesticide	<i>Apis</i>	Chronic	Tan et al. (2017)
Pesticide	<i>Apis, Bombus</i>	Acute	Siviter et al. (2019)
Pesticide	<i>Bombus</i>	Acute	Muth et al. (2019)
Pesticide	<i>Bombus</i>	Acute, chronic	Stanley et al. (2015)
Pesticide	<i>Bombus</i>	Chronic	Smith et al. (2020)
Pesticide	<i>Bombus</i>	Chronic	Lämsä et al. (2018)
Pesticide	<i>Bombus</i>	Chronic	Phelps et al. (2018)
Pesticide, coexposure	<i>Apis</i>	Chronic	Colin, Plath, et al. (2020)
Parasite	<i>Bombus</i>	Acute	Gómez-Moracho et al. (2022)
Parasite	<i>Bombus</i>	Acute	Martin et al. (2018)
Pollution	<i>Apis</i>	Acute	Monchanin et al. (unpublished)
Pollution	<i>Apis</i>	Acute	Monchanin, Drujon, et al. (2021)
Pollution	<i>Apis</i>	Chronic	Monchanin, Blanc-brude, et al. (2021)
Other	<i>Apis</i>	Acute	Wang et al. (2016)
Other	<i>Apis</i>	Acute	Shepherd et al. (2018)
Other	<i>Apis</i>	Chronic	Shepherd et al. (2019)
Coexposure	<i>Apis, Bombus</i>	Acute/Chronic	Piironen and Goulson (2016)
Coexposure	<i>Bombus</i>	Acute/Chronic	Piironen et al. (2016)

The search terms under which each study was found are available in [Table S1](#) in Supporting Information. Five datasets belonging to the authors of this study were also included as they filled the inclusion criteria. These studies measured the impact of stressors on the cognitive performance of bees. The list of the 23 selected studies is available in [Table 1](#).

2.2 | Cognitive tasks

We focused on cognitive data from bees exposed to stressors during their adult life. The effect of stressors on larvae could not be analysed due to the lack of data available (three studies). In all the selected studies, cognitive performance was assessed using associative learning paradigms testing the ability of bees to associate an olfactory or/and a visual stimulus with an appetitive or aversive reinforcement (Giurfa, 2007). Olfactory learning was tested in 18 out of the 23 studies. These studies used learning protocols based on the appetitive conditioning of the proboscis extension response (PER; 16 studies) or the aversive conditioning of the sting extension response (SER; 2 studies). Either response was conditioned by

presenting bees with a conditioned stimulus (an odour) reinforced with an unconditioned stimulus (sucrose solution or electric shock), for 3–15 trials in appetitive assays and 5–6 trials in aversive assays. Trainings included absolute learning (the odour is reinforced) and differential learning (an odour is reinforced; the other is not). Visual learning was tested in 5 out of the 23 studies. These studies used appetitive conditioning protocols in a Y-maze or on artificial flowers (i.e. feeders), or aversive conditioning protocols with electric shocks. One of these studies applied a multimodal appetitive conditioning combining both odour and colour cues to be learnt by bees in an array of artificial flowers (Muth et al., 2019). Here, again bees were tested for differential learning.

2.3 | Stressors

Stressor types covered different pesticides, parasites, predator odours, alarm pheromones, and heavy metal pollutants. Experiments performed with pesticides whose median lethal dose (LD50; i.e. dose that kills 50% of the population) could not be identified in the literature were excluded from our final selection.

2.4 | Exposure duration

In all the studies, stressors were applied before the cognitive tests, except in one study in which it was used as the conditioning stimulus to be learned (i.e. alarm and predator pheromones, Wang et al., 2016). We categorized the duration of exposure using the common dichotomy between acute and chronic exposures. An acute exposure was characterized by a single administration of the pesticide to each individual bee. When bees were exposed to the pesticide more than once, either as a substance present in their environment or as a food directly offered to each individual, the exposure type was considered chronic.

2.5 | Bees

This study did not require ethical approval. The bee species studied in the selected publications were the honey bees *Apis cerana* and *Apis mellifera*, and the bumblebees *Bombus impatiens* and *Bombus terrestris*. These species were not selected purposefully but rather emerged as the species most represented in our dataset from the refinement obtained with other inclusion criteria. We considered bee genus *Apis* or *Bombus* for the analyses.

2.6 | Dataset organization and normalization of variables

All but three raw datasets were available online with the published material. Those three datasets were kindly provided by their authors, that is, Dara Stanley and Ken Tan. The raw data were downloaded and saved as .csv files. A new dataset was created, which combined information on the species, the cognitive task studied, the type of stressor, the type of exposure (acute/chronic), and, in the case of pesticide studies, the dose ($\mu\text{g}/\text{bee}$) or concentration (ppb). The dose (acute exposure) and concentration (chronic exposure) were normalized as the percentage of the LD50. When learning performance was measured as a binary response (e.g. success vs. failure) across multiple trials, the raw data were used to calculate a learning score for each individual corresponding to the number of successful trials. This was required because the variance in binary variables can be mathematically predicted from the mean and sample size and does not reflect biological variance (see Figure S1 in Supporting Information). Each study provided individual cognitive scores for at least one experimental treatment and control group. There was a total of 73 experimental treatments across the 23 studies.

To compare the mean cognitive performance and the cognitive variability across studies, we used a standardized method for the meta-analysis of variation (Nakagawa et al., 2015; Senior et al., 2020). This method controls for the mean–variance linear relationship that may exist in a dataset by using unbiased effect size statistics of the mean and variability, i.e. the natural logarithm of the ratio between the means (lnRR) and the natural logarithm of the ratio between

the coefficients of variation (lnCVR) of treated and control groups, respectively. Changes in lnCVR are not an indirect consequence of changes in lnRR, as would have been the case had we analysed the variance and the mean, but they rather reflect changes in variability per se.

The two prerequisites for this method are (i) to use log scale data and (ii) to observe a mean–variance linear relationship. Studies for which negative cognitive scores were present were transformed to log-scale data by adding the minimum score to all individuals. The mean and standard deviation of the cognitive scores, as well as sample sizes, were calculated for each experimental treatment and control group. A linear relationship and positive correlation were found between the log sample mean and standard deviation in our dataset (see Figure S2 in Supporting Information). All prerequisites being met, we then calculated the lnRR and lnCVR for each experimental treatment and control group (i.e. 73 effect sizes) as well as their sampling (error) variance using equations corrected for the sample size described in (Senior et al., 2020). Individual bees in control and treated groups in all study designs were considered independent.

2.7 | Data analyses

All analyses were conducted in R Studio v.1.2.5033 (RStudio Team, 2015). The code is available. The package METAFOR (Viechtbauer, 2010) was used to compute multilevel meta-analytic models (MLMA), multilevel meta-regression models (MLMR) and to generate forest plots. The study and experiment identifier were always set as nested random effects. For MLMR and depending on the question, the type of stressor, the genus, the type of task, the exposure duration and/or the percentage of LD50 were defined as fixed effects. The restricted maximum likelihood approach (REML) was used to estimate the parameters of the meta-analysis models. Forest plots were used to show the effect size estimates lnRR and lnCVR and their 95% confidence interval (CI). In this approach, positive effect sizes reflect higher means (lnRR) or coefficients of variation (lnCVR) in the treated group compared with controls. Negative effect sizes reflect lower means (lnRR) or coefficients of variation (lnCVR) in the treated group compared with controls. Effects are significant when the 95%CI does not span across the zero line.

3 | RESULTS

3.1 | Stressors reduced cognitive performance and increased inter-individual variability

We first explored the overall effects of stressors on the cognitive performance and its variability among bees across the 23 studies (Figure 1). As expected from previous studies, cognitive scores were significantly reduced following exposure to stressors (MLMA, lnRR = -0.235, 95% CI = -0.323 to -0.147). By contrast,

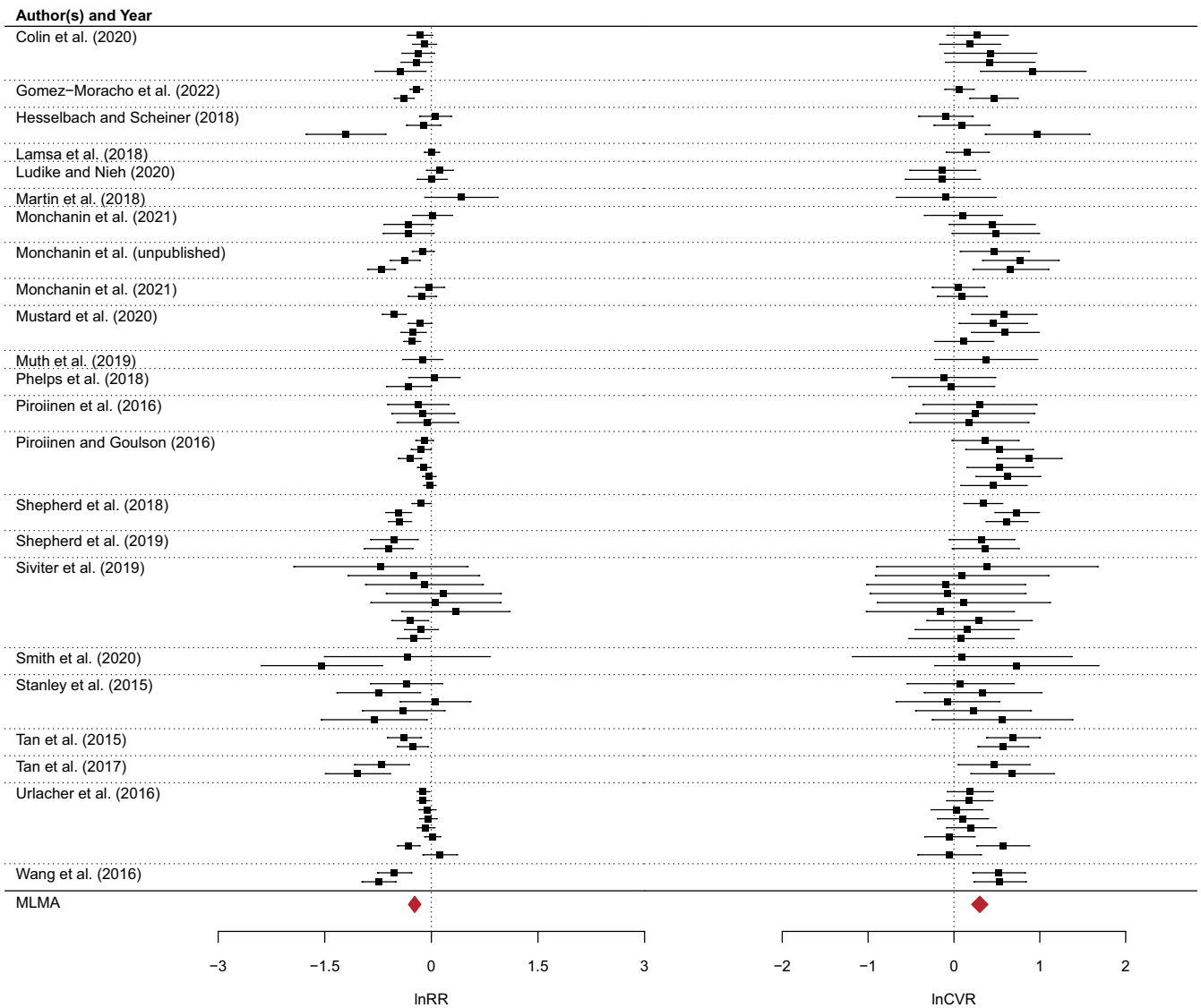


FIGURE 1 Stressors decreased the mean cognitive performance and increased cognitive variability among bees. Forest plots showing the effect size estimates for the mean (lnRR; left panel) and variability (lnCVR; right panel) across the 23 studies. The 95% confidence intervals are displayed for each experiment. Intervals not crossing the zero line reflect a significant effect of the stressors. The red diamonds are estimates from multilevel meta-analysis (MLMA).

the coefficients of variability were increased in treated groups compared with controls (MLMA, lnCVR=0.301, 95% CI=0.207 to 0.396).

These effects on cognitive mean and variability were robust and consistent for most stressor types, bee genus and type of cognitive tasks (Figure 2). Treated groups exhibited lower cognitive scores and higher coefficients of variation than controls regardless of the type of stressor (Figure 2a; MLMR, lnRR: QM=2.078, $df=4$, $p=0.722$, lnCVR: QM=3.791, $df=4$, $p=0.435$), the bee genus (Figure 2b; MLMR, lnRR: QM=1.111, $df=1$, $p=0.292$, lnCVR: QM=0.343, $df=1$, $p=0.558$) and the type of cognitive task (Figure 2c; MLMR, lnRR: QM=4.696, $df=3$, $p=0.196$, lnCVR: QM=5.056, $df=3$, $p=0.168$). There was no significant interaction between these variables on the lnRR (MLMR, $stressor*genus$: QM=0.123, $df=1$, $p=0.726$, $stressor*task$: QM=1.860, $df=2$,

$p=0.395$, $genus*task$: QM=1.086, $df=1$, $p=0.297$) and the lnCVR (MLMR, $stressor*genus$: QM=0.015, $df=1$, $p=0.902$, $stressor*task$: QM=0.165, $df=2$, $p=0.921$, $genus*task$: QM=1.735, $df=1$, $p=0.188$).

3.2 | Variability in cognitive performance increased with stressor intensity

To investigate whether stressor intensity modulates the effects of stressors on the variability of the cognitive performance, we focused our analyses on the 14 pesticide studies of our dataset for which the percentage of LD50 was known (Figure 3). Pesticide studies were the most abundant in the literature and present the advantage that a normalization of stressor intensity across drugs

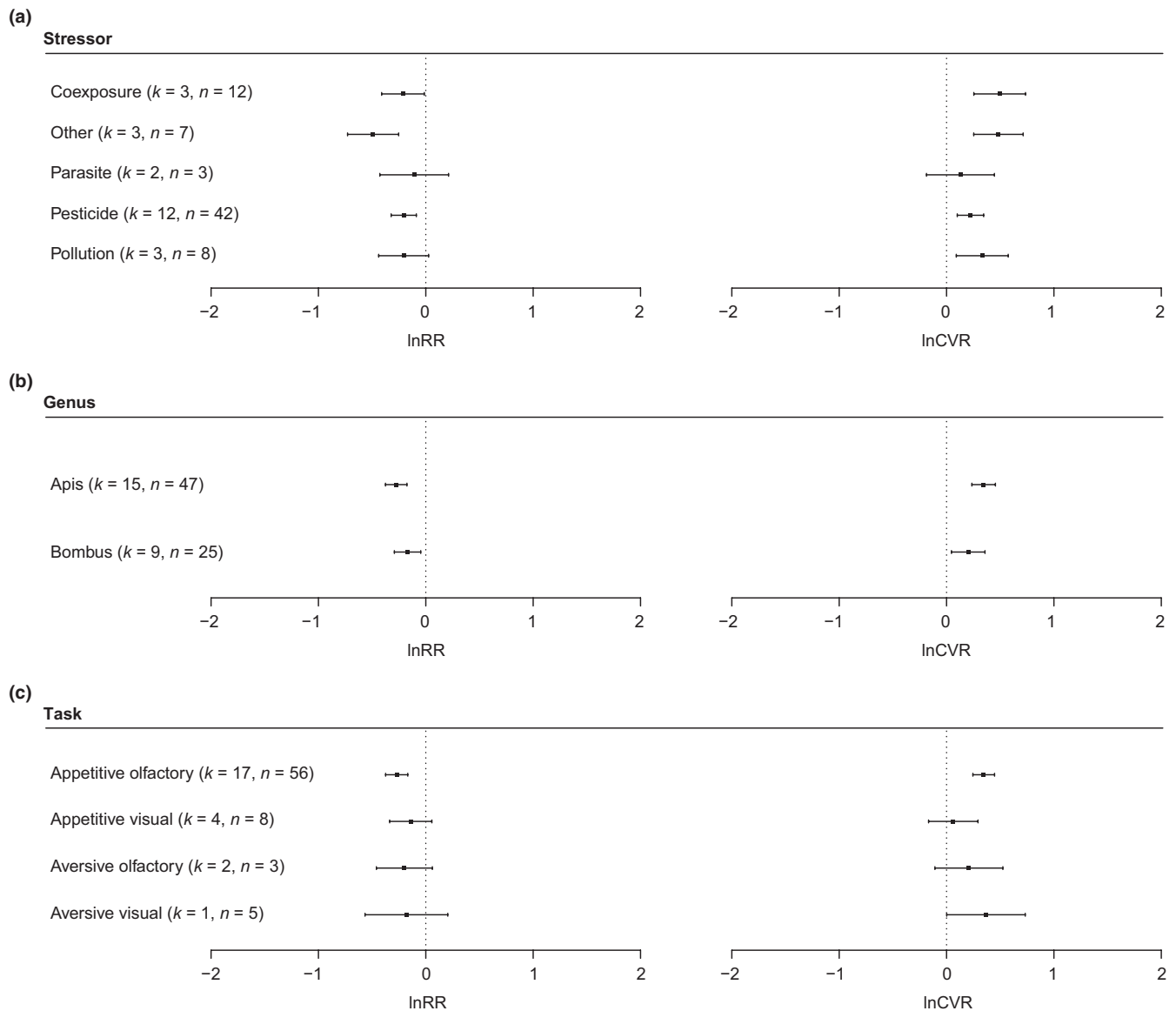


FIGURE 2 Effect of stressors on the cognitive mean and variability were consistent across experimental designs. Forest plots showing the mean effects size estimates lnRR (left) and lnCVR (right) for (a) different types of stressors, (b) different bee genera and, (c) different cognitive tasks. The 95% confidence intervals are displayed and indicate a significant effect of the stressor when not crossing the zero line. Number of studies (k) and number of effect sizes (n) are given for each subgroup.

was possible using LD50s and durations of exposure (acute or chronic).

Both acute and chronic exposures reduced the cognitive scores of bees (Figure 3a; MLMA, acute: $\lnRR = -0.139$, 95% CI = -0.267 to -0.012 ; chronic: $\lnRR = -0.480$, 95% CI = -0.693 to -0.268) and increased the coefficients of variability (MLMA, acute: $\lnCVR = 0.204$, 95% CI = 0.029 to 0.379 ; chronic: $\lnCVR = 0.405$, 95% CI = 0.131 to 0.679). Chronic exposure had a significantly stronger detrimental effect on the cognitive scores of bees compared with acute exposure (MLMR, \lnRR : $QM = 5.575$, $df = 1$, $p = 0.018$). Yet, the impact of pesticides on cognitive variability was not sensitive to exposure duration (MLMR, \lnCVR : $QM = 1.538$, $df = 1$, $p = 0.215$).

To further explore whether the effects of stressors on mean performance and cognitive variability differed with stress magnitude,

we analysed different doses of pesticide (Figure 3b). A dose-dependent effect was found on the cognitive scores and on the coefficients of variation. While the mean cognitive scores in treated groups decreased with increasing doses (MLMR, \lnRR : $QM = 11.470$, $df = 1$, $p < 0.001$), the coefficients of variation increased (MLMR, \lnCVR : $QM = 6.536$, $df = 1$, $p = 0.011$). There was no significant interaction between the dose and the duration of exposure on both estimates (MLMR, $exposure \times dose$, \lnRR : $QM = 3.658$, $df = 1$, $p = 0.056$, \lnCVR : $QM = 3.069$, $df = 1$, $p = 0.080$). This means pesticides were on average more detrimental to cognitive performance at high doses, yet inducing a greater variability, irrespective of exposure duration. These opposite effects of stressor intensity on \lnRR and \lnCVR triggered an indirect negative correlation between the two estimates in the whole dataset (Pearson's correlation test, $r = -0.667$, $p < 0.001$).

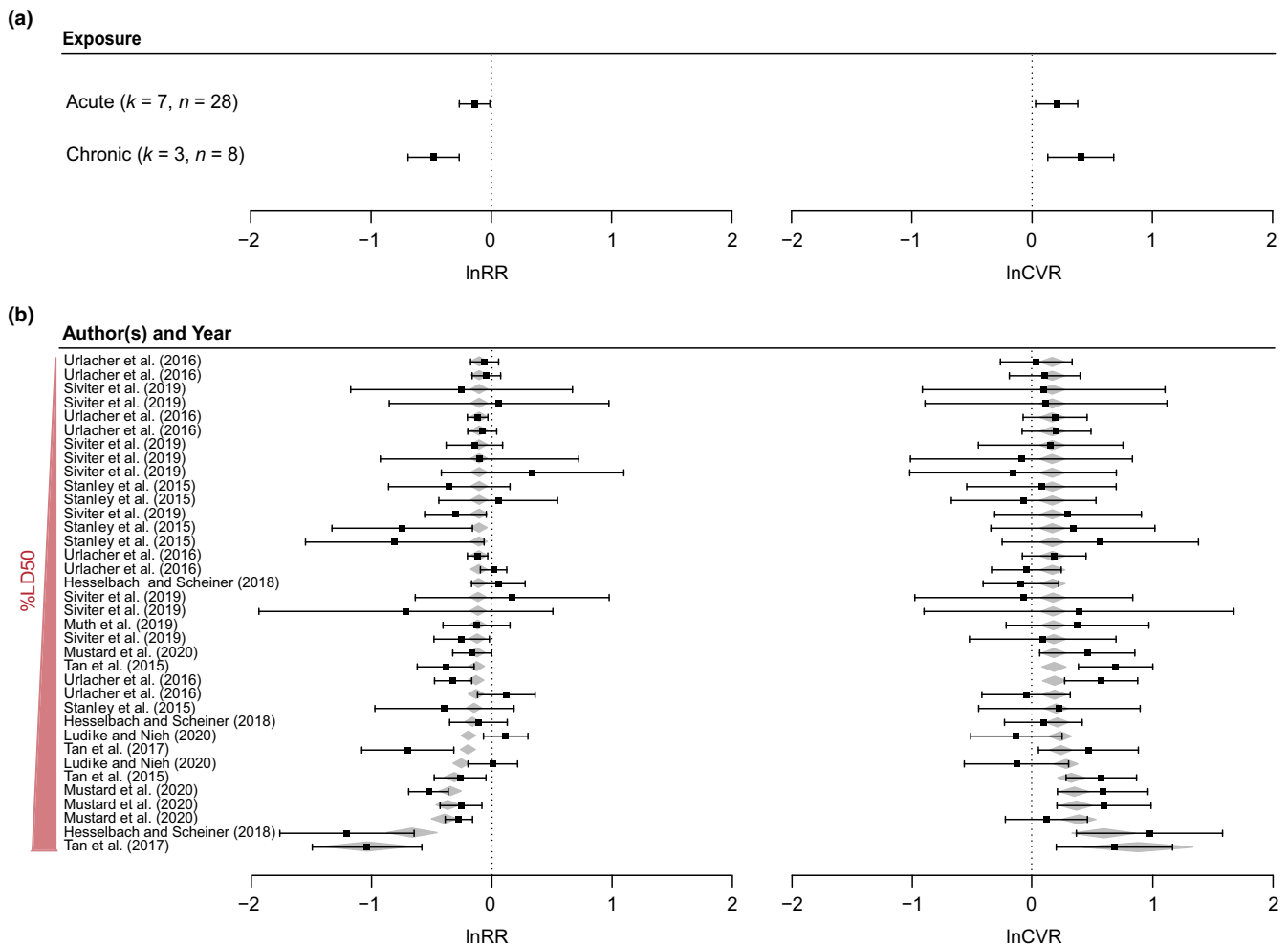


FIGURE 3 Stressor intensity differentially affected the mean cognitive performance and its variability among bees. Forest plots showing the mean effects size estimates of the cognitive mean (lnRR, left) and variability (lnCVR, right) for bees treated with pesticides at (a) different exposure duration, and at (b) different doses. The 95% confidence intervals are displayed and indicate a significant effect of the pesticide treatment (either duration or intensity) when not crossing the zero line. The grey diamonds are estimates from multilevel meta-analysis (MLMA).

4 | DISCUSSION

Many environmental stressors affect the behaviour and cognition of animals (Killen et al., 2013; Klein et al., 2017; Siviter et al., 2018, 2021). While studies reporting such sublethal effects have typically focused on mean phenotypic traits, all individuals in a population are not similarly affected by stressors, and the resulting phenotypic variability may be critical for stress resilience. Here we tested this hypothesis by analysing raw datasets of 23 bee studies. We showed different effects on the cognitive mean and inter-individual variability of insects exposed to stressors, depending on stress level and exposure mode, thus raising the importance of examining variability in addition to mean phenotypic traits in ecotoxicological studies.

Focusing on pesticides revealed the mean cognitive performance of bees was altered by both chronic and acute exposures, with strongest effects observed after a chronic exposure. This result is consistent with a previous meta-analysis (Siviter et al., 2018). However, the

variability in cognitive performance between bees was increased by both exposure durations. This means some bees were better able to cope than others with the pesticide exposure regardless of its duration. This is, to our knowledge, the first study showing stress-induced variation in learning performances in an animal.

Such variability in response to stress might reflect inter-individual variability in the efficiency of homeostatic physiological processes that can counteract the effect of pesticide exposure to the drug (Cohen, 2006). Indeed most pesticides act on the nervous system of bees whose plasticity to maintain homeostasis is well-known (Cabirol & Haase, 2019; Turrigiano & Nelson, 2000). For instance, neurons can compensate a change in the balance between brain excitation and inhibition by modulating the efficacy of specific synapses (Poza & Goda, 2010). As neonicotinoid pesticides activate the excitatory cholinergic neurotransmission pathway, one might expect the brain to counteract this increased excitation (Cabirol & Haase, 2019). Future toxicity assessments should also consider the long-term consequences of stressors on phenotypic variability.

Indeed, a recent study showed a delayed impact of an acute exposure to the pesticide sulfoxaflor on the foraging behaviour of bees (Barascou et al., 2022).

Interestingly, cognitive performance and variability among bees varied in opposite directions with increasing doses of toxic compounds. The strong reduction of cognitive scores by high doses advocates for the use of lower pesticide concentrations in the field. Reducing use to doses having sublethal effects on target pest insects would still protect crops when pest density is low and thereby would be less damaging to non-target insects such as pollinators (Colin, Monchanin, et al., 2020).

Cognitive and behavioural variability is thought to be particularly important for populations' resilience after environmental changes (Jandt et al., 2014) as it augments the probability that some individuals display adapted behaviour to the new environmental conditions. In group-living species, such as social honey bees and bumblebees, the high diversity of behavioural phenotypes within colonies is known to improve the efficiency of collective decision-making and the ability of groups to find optimal solutions to changing conditions (Burns & Dyer, 2008). The observed increase in cognitive variability following exposure to pesticides suggests that some individuals have maintained sufficient cognitive abilities to support efficient foraging (Klein et al., 2017). Most doses were far below the LD50 and one might expect that higher doses would reduce variability as most individuals would be affected by the drug. This suggests incorporating an analysis of variability in the risk assessment procedures of new plant protection products (PPPs) would help refining the risk diagnostic and identifying the upper doses at which most animals are affected, and the population resilience is endangered. However, the link between cognitive variability measured in laboratory assays and colony success should still be experimentally demonstrated.

In nature, bees often encounter pesticides over long time periods especially when colonies are located near treated crops and in the hive due to the residues present in the honey and wax (Godfray et al., 2014, 2015; Tsvetkov et al., 2017). The consequences of such a chronic exposure to pesticides are often not a priority in risk assessment procedures. Policy regulations in the European Union and the United States regarding the commercialization of new PPPs ask for acute toxicity assays on bees and other non-target animals before asking for chronic toxicity assays (EPPO, 1992, 2010; U.S. Environmental Protection Agency & Code of Federal Regulations (CFR), 2010). Only when acute toxicity is significant would a chronic toxicity assay be performed. Although the European Food Safety Authority recommends the inclusion of chronic exposure assays earlier in the risk assessment procedure, such assays are not yet mandatory (EFSA, 2013). The effects of PPPs that will be encountered chronically in the field might, therefore, be underestimated. Our study provides an additional argument for the inclusion of chronic assays, alongside acute ones, in the risk assessment procedures of new PPPs. Note that the fact similar results were obtained in *Bombus* and *Apis* confirms honey bees are overall suitable surrogates for non-*Apis* species in regulatory risk assessments of pesticide toxicity (Arena & Sgolastra, 2014; Heard et al., 2017; Thompson & Pamminger, 2019),

as currently considered by the European commission (EPPO, 2010). This is true at least when exploring general trends. But these results must then be complemented by more detailed studies on non-*Apis* bee species that may vary in their sensitivity to pesticides (Arena & Sgolastra, 2014).

Overall, our study highlights a differential effect of chronic and acute exposures to pesticides as well as an important influence of the stressor intensity on the proportion of individuals that might be impacted. Focusing on variability helped identify chronic stress conditions bees may not be able to cope with, which could not be done by looking at the mean only. Interestingly all types of stressors similarly influenced bee cognition. Except for studies performed with parasites, the mean cognitive scores were severely impacted by all stressors, and the coefficient of variation was increased. This means stress can favour the diversification of cognitive abilities (Badyaev, 2005), an observation already made in rodents where mild stressors can have beneficial effects on the cognitive performance (Hurtubise & Howland, 2016). These intriguing effects of stress on cognitive traits demonstrate the importance of considering inter-individual phenotypic variability in analyses of the impact of environmental stressors on animals. We hope such an approach can be generalized to assess more thoroughly the hazardous nature of the stressors and identify the modes of exposure that might be less damaging for wild populations. An effort should be made to apply the analysis of phenotypic variability to studies on bee pathogens and parasites as they are strongly associated with population decline and yet represented only three experiments in our dataset (Dainat et al., 2012; Fürst et al., 2014). Future investigations should also consider the possible interaction between agrochemicals, which have synergistic effects on bee mortality, but antagonistic effects on behaviour when looking at the mean only (Siviter et al., 2021). Ultimately the results of such studies should lead to explicit guidelines for farmers on the safe use of these toxic substances.

AUTHOR CONTRIBUTIONS

Amélie Cabirol, Tamara Gómez-Moracho, Cristian Pasquaretta and Mathieu Lihoreau designed the study. Amélie Cabirol, Tamara Gómez-Moracho and Coline Monchanin collected the data. Tamara Gómez-Moracho processed the data and prepared dataset. Amélie Cabirol, Tamara Gómez-Moracho, Coline Monchanin and Cristian Pasquaretta analysed the data. Amélie Cabirol wrote the first draft of the manuscript. All authors substantially contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available from Dryad Digital Repository: <https://doi.org/10.5061/dryad.63xsj3v72> (Cabirol et al., 2023b). The R code used for the analyses is available on Zenodo: <https://doi.org/10.5281/zenodo.7794106> (Cabirol et al., 2023a).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Analysis of variance in studies with binary data. (A) Impact of a pesticide and parasite on bumblebees' learning performance measured with a classical conditioning of the proboscis extension response (PER) (from Piironen et al., 2016). The percentage of individuals that extended the proboscis in response to the conditioned stimulus (i.e. percentage of learners) is plotted across 10 successive learning trials. (B) Matrix representing the impact of a stressor on the variance in learning performance. For an equal sample size in the control and treated groups, the impact of the stressor on variance can be calculated using the mean of both control and treated groups. An increased (orange) or decreased variance (blue) can be predicted.

Figure S2. Linear relationship between the log sample mean and standard deviation of cognitive scores in control (black dots) and treated (white dots) groups. A significant positive correlation was found between the two variables (Pearson's correlation test: $r = 0.424$, $p < 0.001$).

Table S1. Results of the PubMed search for studies measuring the impact of stressors on the cognitive performance of bees. Crosses indicate the search terms under which each study included in the final dataset was found.

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