

1 **Intraspecific variation in invertebrate cognition: a review**

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33 **Abstract**

34 A well-established field of research in vertebrates focuses on the variability of
35 cognitive abilities within species. From mammals to fish, numerous studies have revealed
36 remarkable differences in the cognitive phenotype among individuals, particularly in terms of
37 sex or personality. However, many aspects of the mechanisms, genetics, and selective
38 pressures that underlie individual cognitive variation remain unclear. Surprisingly,
39 intraspecific variability in cognition has received much less attention in invertebrates, despite
40 the increasing evidence of remarkable cognitive abilities in this group and the insights that
41 could be gained from examining simultaneously two distinct taxa, namely vertebrates and
42 invertebrates. In this review, we provide evidence that certain invertebrate species exhibit all
43 the key features of cognitive variation observed in vertebrates, including differences related
44 to sex and personality. In many cases, invertebrate studies have provided insights into the
45 genetic basis, evolvability and response to selection of cognitive variability. Moreover, we
46 highlight evidence for caste differences in eusocial insects, which are linked to task
47 specialisation within the colony. This makes insect eusociality a valuable system for
48 understanding how selection influences cognitive variation. We propose that cognitive
49 variation in invertebrates may be more widespread than currently thought, and that selection
50 may operate in a similar manner on two distantly related cognitive systems (vertebrates and
51 invertebrates). Finally, we suggest that invertebrates hold the potential to serve both as
52 alternative and complementary models to vertebrates, contributing to a deeper understanding
53 of cognitive evolution.

54

55 **Keywords:** behavioural syndrome; cognitive ecology; cognitive evolution; individual
56 differences; personality; invertebrate cognition.

57 **Introduction**

58 Interindividual variability has been a hallmark of research in human psychology (e.g.,
59 Conway and Kovacs 2013; Humphreys 1979; Maltby et al. 2010), and for at least three
60 decades in animal behavioural biology (e.g., Carere and Maestripieri 2013; Laskowski et al.
61 2022; Wilson 1998). We now know that intraspecific variability in cognitive abilities is not
62 exclusive to our species, but it has been found in a number of mammalian (Banerjee et al.
63 2009), avian (Ashton et al. 2018; Cole et al. 2011), and teleost fish species (reviewed in
64 Lucon-Xiccato and Bisazza 2017), and based on initial evidence in some reptiles (e.g.,
65 Carazo et al. 2014).

66 Several disciplines are interested in intraspecific variability in animal cognition,
67 including comparative psychology, neuroscience, applied ethology, and pharmacology, as
68 well as cognitive ecology. From the latter perspective, there are at least three reasons for this
69 interest. First, individual differences in cognition are likely associated with individual
70 differences in fitness (e.g., Ashton et al. 2018; Cole and Quinn 2012, Cole et al. 2012; Smith
71 et al. 2015). Second, the well-known interspecific differences in cognition are thought to have
72 evolved mostly through selection acting on intraspecific variation. Third, because many
73 cognitive traits are expected, at least hypothetically, to enhance an animal's interaction with
74 its environment (Preiszner et al. 2017), their variation, including phenotypic plasticity driven
75 by experience (Cauchoix et al. 2020; Dukas 2004; Montalbano et al. 2022), is a potentially
76 relevant process in coping with responses to anthropogenic impacts. These reasons for
77 interest, together with those related to other topics such as animal welfare (Berry et al. 2015;
78 Mather and Carere 2019) and precision psychiatry (Fernandes et al. 2017), make the study of
79 intraspecific variation in cognition particularly relevant.

80 However, despite the emphasis and growing literature on intraspecific cognitive
81 variability in vertebrates, this phenomenon has received less attention in invertebrates, where

82 averaging has long obscured individual variation. This is surprising given that already in the
83 early 20th century, the pioneering psychologist Charles Turner found that displaced homing
84 ants differed in how quickly they returned to their nests, which he explained by suggesting
85 there were individual differences in memory (Turner 1907). Furthermore, research on
86 invertebrate cognition has expanded considerably over the last few decades, often yielding
87 novel and significant insights (reviewed in Chittka and Skorupski 2011; Menzel and Giurfa
88 2001; Perry et al. 2016; Perry et al. 2017; Vallortigara 2020). Similar advances in
89 understanding cognitive variance could be achieved if invertebrate models were fully
90 integrated. While vertebrate and invertebrate brains share several basic mechanisms (Cayre et
91 al. 2002; Kammermeier and Reichert 2001), they also exhibit major differences that can be
92 exploited for complementary research goals. Compared to vertebrates, invertebrates often
93 provide tractable and accessible models because of their relatively simple nervous systems
94 and a genetic background that is easy to manipulate. This has allowed researchers to carry out
95 experiments in invertebrates that would be difficult or impossible with vertebrates, which
96 have more complex nervous systems and ethical constraints. Invertebrates also have shorter
97 life spans, allowing researchers to easily observe and manipulate behaviour over several
98 generations. In addition, invertebrates are often less expensive to maintain and breed, making
99 them ideal for large-scale studies. Therefore, studying cognitive variability in two systems
100 with some degree of difference is likely to be advantageous for identifying general
101 evolutionary phenomena.

102 The aim of this review is to provide a collection of evidence for intraspecific cognitive
103 variability in invertebrates, focusing on three typical explanatory factors of variation reported
104 in vertebrates: sex differences, individual differences, and cognition-personality covariation
105 (Fig. 1). Thereafter, the review aims to highlight one remarkable example of cognitive
106 variation observed in eusocial insects that is lacking in vertebrates, that is caste-associated

107 cognitive variation (Fig. 1). The literature search was conducted on Scopus and Google
108 Scholar, with relevant keywords ('sex differences' + 'cognition' + 'invertebrates', 'individual
109 differences' + 'cognition' + 'invertebrates', 'personality' + 'cognition' + 'invertebrates',
110 'caste' + 'cognition' + 'invertebrates') and by checking references and citations of the articles
111 retrieved. In each of the aforementioned sections, the review additionally discusses a number
112 of potential advantages of invertebrate research, which could become powerful,
113 complementary tools for studying cognitive evolution alongside vertebrate models.

114

115 **Sex differences**

116 Cognitive sex differences have been reported in a number of vertebrate species and
117 for a range of abilities (reviewed in Jonasson 2005; Jones et al. 2003; Lucon-Xiccato 2022).
118 This research has focused on two main lines of investigation complementary to a full
119 understanding of the evolution of cognitive sex differences: cognitive ecologists have been
120 particularly interested in understanding the adaptive explanations for sex differences, while
121 physiologists have devoted considerable attention to the underlying neuroendocrine
122 mechanisms. The evidence reported below suggests a role for invertebrates in the study of
123 both adaptive explanations and underlying mechanisms of cognitive sex differences.

124

125 *Adaptive value of cognitive sex differences*

126 The main adaptive explanation for cognitive sex differences relates to differential
127 behaviour, life history, and ecology of the two sexes, which might determine sex-specific
128 requirements (e.g., Astiè et al. 1998; Gaulin and Fitzgerald 1986; Lucon-Xiccato et al. 2016).
129 For instance, if in a particular species, one sex (but not the other) is required to perform a
130 certain cognitive task, selection could favour the evolution of a greater ability to solve such
131 task in that sex. Invertebrates can potentially contribute significantly to test this hypothesis

132 considering that some groups display large sexual dimorphism (e.g., Hopkins and Kopp
133 2001; Thornhill and Gwynne 1986). Moreover, it would interesting to understand whether the
134 response to selection for sexual differentiation of cognition is similar in invertebrates and
135 vertebrates.

136 Spatial behaviour and ecology are among the most investigated functional contexts in
137 which cognitive sex differences emerge in vertebrates (reviewed in Jones et al. 2003). They
138 have also been studied in a few invertebrate species. In a cephalopod mollusc, the cuttlefish
139 *Sepia officinalis*, males range over a larger area, suggesting greater spatial abilities than
140 females. Jozet-Alves and colleagues (2008) tested this prediction in a T-maze spatial learning
141 task: the cuttlefish had to enter one arm of the maze, either the right or the left, indicated by a
142 visual cue, to reach a ‘comfortable’ habitat. Male and female cuttlefish showed no difference
143 in the speed at which they learned the task. However, probe trials demonstrated that males
144 learned to choose the correct arm by using egocentric cues (right or left), whereas females
145 used the visual cue. This aligns with findings in vertebrates, including humans, suggesting
146 that selection may determine sex differences in spatial navigation strategy (Chai and Jacobs
147 2009; Rodríguez et al. 2010). Our literature search also showed that that spatial learning and
148 strategy have been investigated in two other invertebrate species, with no evidence of sex
149 differences (crayfish *Orconectes rusticus*: Tierney and Andrews 2013; texas field crickets
150 *Gryllus texensis*: Kozlovsky et al. 2022).

151 In some vertebrate species, it has been hypothesised that cognitive sex differences
152 may arise in relation to the reproductive strategy (Laland and Reader 1999). This idea has led
153 to a study of the Japanese pygmy squid *Idiosepius paradoxus* (Takeshita and Sato 2016).
154 Eggs in this species can exceed five times the weight of the female’s body, determining
155 higher energy requirements and possibly a different foraging decision-making system
156 compared to males. Accordingly, Takeshita and Sato demonstrated that females tend to

157 overestimate their optimal prey size, while males tend to underestimate it. Another sex
158 difference in judgment has been described in the field cricket *Gryllus integer* in the context of
159 reproduction (Leonard and Hedrick 2009). When presented with a simultaneous choice
160 between recordings of conspecific calls, both males and females preferred calls with long
161 elements. However, only females showed such a preference when the calls were presented in
162 isolation. This suggests that female crickets use an absolute rule to estimate call length,
163 whereas males use a comparative strategy. Finally, in a study on the fruit fly *Drosophila*
164 *melanogaster*, males were maintained in a regime of either monogamy or polygamy for 100
165 generations (Hollis and Kawecki, 2014). Polygamous males were able to learn to discriminate
166 between receptive and unreceptive females, while monogamous males were not.
167 Monogamous males also failed to learn an aversive olfactory conditioning task. Although it
168 does not provide a direct investigation of sex differences, the fruit fly study suggests that
169 different reproductive scenarios affect cognitive abilities of one sex.

170 A third recognised context in which cognitive sex differences in vertebrates arise is
171 sociality (Choleris and Kavaliers, 1999; Geary 2022; Lucon-Xiccato et al. 2016). In many
172 species, males and females live in different social environments, determining selection for
173 solving different social tasks. For instance, in a fish species in which females are more social
174 than males, the females judged more efficiently the size of social groups (Lucon-Xiccato et
175 al. 2016). While we are not aware of direct studies in invertebrates, one paper has
176 hypothesised a similar role for social behaviour. Whitehouse (2016) found a greater ability to
177 learn a novel foraging technique in males than females of the group-living spider *Argyrodes*
178 *antipodanus* proposing that sex differences may be related to the increased complexity of
179 males' intrasexual interactions. Indeed, males are reported to compete for access to both food
180 and reproductive partners, often learning to adapt flexibly to new winner-loser relationships.

181 Besides the hypothesis-testing studies mentioned above, we found relevant research
182 conducted using a more descriptive approach (e.g., conditioning learning in mosquitoes:
183 Sanford and Tomberlin 2011). The results of these studies are in some cases difficult to
184 interpret. For example, domestic crickets *Acheta domesticus* showed sex differences in an
185 olfactory learning task (Albers and Reichert 2022) but not in a shuttle-box avoidance learning
186 task (Stauch et al. 2021), a difference that could be due to methodological differences
187 between the studies or to task-specific sex differences. One study also suggested that sex
188 differences in learning are expressed only at certain developmental phases (Sanford and
189 Tomberlin 2011). While these exploratory studies are useful in discovering new effects to
190 investigate, the hypothesis-driven approach will certainly advance our understanding of the
191 adaptive significance of cognitive sex differences.

192

193 *Mechanisms of cognitive sex differences*

194 Much of the research on cognitive sex differences of vertebrates aimed to elucidate
195 the proximate mechanisms. While these studies have usually used animals as a model for
196 understanding the human nervous system, their findings are also relevant to disciplines
197 interested in cognitive evolution. Most of the available data on mechanisms involve rodents
198 such as rats and mice (e.g., Brake and Lacasse 2018), and primates (e.g., Bachevalier and
199 Hagger 1991). Overall, these studies have outlined a central role for gonadal hormones in
200 determining sex differences via developmental and/or activation mechanisms. The
201 contribution of other underpinning mechanisms, such as genes and specific neural circuits,
202 remains less understood (e.g., Agate et al. 2003; Dewing et al. 2003).

203 Currently, it is difficult to identify a contribution of invertebrates to the study of sex
204 hormones and cognitive sex differences. Vertebrates' sex steroids are generally absent in
205 invertebrates, although experimental evidence suggests possible biological effects (Köhler et

206 al. 2007) and even enzymes necessary for their synthesis (LaFont 2000). However,
207 invertebrate models may provide complementary insights to what we currently know about
208 other mechanisms of sex differences, although in our search we identified only two relevant
209 studies. In the first study, the nematode *Caenorhabditis elegans* shows an interesting sex
210 difference in learning. Males actively approach hermaphroditic individuals to mate. Sakai and
211 colleagues (2013) found that the males could be conditioned to associate a chemical cue with
212 the presence of hermaphrodites, but hermaphrodites could not. However, hermaphroditic
213 individuals could learn non-sexual associations through conditioning. In the second study,
214 Sammut and colleagues (2015) found expression of the neuropeptide *pdf-1* in a bilateral pair
215 of cells in males, in an area that does not contain known neurons in hermaphrodites. Ablation
216 of these cells prevented sexual conditioning in males. This simple model may be interesting
217 for investigating the development, and possibly evolution, of sex specific neural circuits
218 involved in cognition. A typical neuroscience model, the fruit fly *D. melanogaster*, is also
219 promising in this respect. In this species, approximately 50 % of the genome has sex-specific
220 expression, and studies are already characterising pathways that determine sex differences in
221 behaviour (Jazin and Cahill 2010).

222

223 *Sex differences and caste*

224 Eusocial insects offer a powerful system for studying the evolution of cognitive sex
225 differences, as males and females in this group often exhibit behavioural and sexual
226 dimorphism to a greater degree than vertebrates. These sex differences are ultimately related
227 to the division of labour in colonies, resulting in reproductive and non-reproductive
228 individuals (Oster and Wilson 1978). Our literature review found that bumblebees (*Bombus*
229 *sp.*) have been extensively investigated in this context. Worker bumblebees are sterile
230 females whose primary role is to forage for the colony (Free 1955). This activity requires

231 workers to memorise features and the spatial location of key foraging sites. For this reason,
232 sterile female workers typically look back to memorise the foraging site when they leave.
233 Male bumblebees also forage, but only for themselves, without returning to the colony. The
234 sex differences in bumblebee foraging behaviour suggest that spatial and associative learning
235 may be more important for the sterile female workers than for males, and thus a potential
236 source of sex-specific selection. Separate studies have analysed associative learning in males
237 and sterile female workers of four bumblebee species (*Bombus impatiens*, *B. terrestris*, *B.*
238 *vancouverensis nearcticus*, and *B. vosnesenskii*) and found no sex differences in learning
239 performance (Lichtenstein et al. 2015; Manning et al. 2021; Muth et al. 2021; Wolf and
240 Chittka 2016) and memory retrieval (Lichtenstein et al. 2015). Moreover, factors such as the
241 degree of similarity between cues indicating food sources had comparable effects on learning
242 performance in males and females (Wolf and Chittka 2016). One study also found that males
243 performed learning flights similar to those observed in sterile female workers, likely to
244 remember the location of a food source (Robert et al. 2017). All this suggests that male and
245 worker bumblebees have similar learning abilities and strategies when foraging. However, it
246 should be noted that males responded less quickly to a sucrose reward (Muth et al. 2021) and
247 were less responsive in learning experiments (Manning et al. 2021). Therefore, while the
248 learning system may not show sex differences in this species, the motivational system may do
249 so, with potential indirect effects on learning performance in nature (Rowe and Healy 2014).

250 Understanding sex-specific selection on cognition through sociability is another
251 interesting opportunity offered by studying eusocial species. The wasp *Polistes fuscatus* is
252 particularly attractive for this purpose because males and females display different social
253 behaviour. Female wasps live in cooperative social groups in which individual recognition is
254 critical. Conversely, males leave the colony as adults to find mates. DesJardins and Tibbetts
255 (2018) tested the cognitive hypothesis that follows directly from sex differences in social

256 behaviour: females may have evolved better social skills than males. The results of their
257 study supported this hypothesis. Females outperformed males in a task where they had to
258 recognise conspecifics. The authors elegantly demonstrated that this effect was specifically
259 restricted to social learning by performing an analogous task that involved colour learning in
260 which the two sexes performed similarly. A similar system has been studied in the honey bee
261 *Apis mellifera anatolica*, where workers (sterile females) live in the colony and are highly
262 social, but drones (males) tend to be solitary. Using an aversive learning paradigm, Dinges
263 and colleagues (2013) found greater cognitive performance in the workers. These sex
264 differences may be related to the fact that males are mostly required to find and remember
265 mating sites, while workers are involved in a number of colony-related social tasks.
266 Interestingly another study in the honey bees, *Apis mellifera*, which did not directly compare
267 the two sexes, found that the learning performance of sterile female workers, but not drones,
268 was affected by a chemical cue of social distress (alarm pheromone; Avalos et al. 2017). The
269 two sexes may therefore differ in the way they modulate their response to social cues.

270

271 *Summary of evidence of cognitive sex differences*

272 When compared to other aspects of intraspecific variability, studying sex differences
273 is relatively easier experimentally, as it involves comparing two distinct groups of subjects.
274 This provides a good starting point for understanding cognitive variability in invertebrates.
275 The main finding of this review is that the literature contains some evidence for sex
276 differences in invertebrates. The observed sex differences cover a relatively wide range of
277 cognitive abilities, and, at least in some cases, could be predicted on the basis of sex
278 differences in ecology, reproduction, and behaviour. It is worth highlighting that in one case,
279 the sex difference was found in a specific task and the two sexes had comparable
280 performance in another, similar task (DesJardins and Tibbetts 2018). This leads to the idea

281 that cognitive sex differences in invertebrates arise through selection on specific tasks’
282 performance. However, it is clear that data on cognitive sex differences in invertebrates
283 pertain to very few species and lineages (Fig. 2). Notably, some of the cognitive sex
284 differences were found in invertebrate species with relatively limited sexual dimorphism.
285 Invertebrates with higher levels of sexual dimorphism should be investigated, as they may
286 have much larger cognitive sex differences. Finally, the existence of reproductive and non-
287 reproductive castes within eusocial insect colonies provides another tool for studying sex
288 differences with the advantage of potentially discerning between the effects of sex and the
289 effect of reproductive status.

290

291 **Individual differences**

292 In vertebrates, attention has been devoted to a form of cognitive variation that is more
293 subtle than sex differences. Individuals (even of the same sex) often perform differently on
294 cognitive tasks in a range of species, from tetrapods (e.g., Thornton and Lukas 2012) to
295 teleosts (reviewed in Lucon-Xiccato and Bisazza 2017). These differences could be due to
296 random measurement fluctuations but also to a number of genetic and ontogenetic factors. If
297 the differences have biological significance, they should have at least two characteristics.
298 First, they should be statistically repeatable over time (i.e., temporal consistency; Cauchoix et
299 al. 2018; Rowe and Healy 2014). In other words, the rank order of performance should be
300 virtually constant when a set of individuals is tested multiple times in the same cognitive task.
301 This repeatability approach has been initially applied to study behavioural variation and
302 personality and can be implemented in different manners, from the use of simple correlations
303 to mixed-effects modelling (e.g., O’Dea et al. 2021). More recently, studies in vertebrates
304 have begun to adopt the within-task repeatability approach to identify individual differences
305 in cognition (Ashton et al. 2022; Davidson et al. 2022; De Meester et al. 2022b; Lucon-

306 Xiccato et al. 2020a). Second, when individuals are tested in two or more different tasks that
307 arguably involve the same cognitive function, individual differences with biological
308 significance should result in a positive correlation of the performance between tasks (e.g.,
309 Montalbano et al. 2020). Repeatability within and between tasks is considered evidence of
310 cognitive individual differences that have biological significance and cannot be regarded as
311 random fluctuations in performance (Rowe and Healy 2014). This is a prerequisite for
312 considering their importance for fitness and evolutionary processes.

313

314 *Repeatability of cognitive performance*

315 Surprisingly, there has been little emphasis on formally testing the two forms
316 repeatability of cognition that are indicative of individual differences in vertebrates. Our
317 review identified only four studies that tested within-task repeatability. In the first study, the
318 behaviour of *Frontinella communis* spiders after removal of prey from their webs was
319 observed to infer the subjects' mnemonic abilities (Rodríguez and Gloudeman 2011). The
320 spiders' search behaviour was highly repeatable, suggesting individual differences in the
321 mnemonic abilities involved in the task. Finke and colleagues (2021) demonstrated within-
322 task repeatability of individual honey bee performance in visual (shape) discrimination tasks.
323 In the same species, consistent learning abilities were recently found for simple visual, simple
324 odour, and complex visual discrimination tasks (Finke et al. 2023). The last study showed
325 that in the ant *Aphenogaster senilis* tool use by workers was a repeatable performance across
326 trials (Maák et al. 2020).

327 Regarding between-tasks repeatability, few relevant studies were identified in the
328 invertebrate literature. One of these studies involved *D. melanogaster* flies (Smith et al. 2022)
329 that were tested with different olfactory aversive conditioning tasks, consisting of learning
330 the association between an odour and a shock and between an odour and a bitter taste. In line

331 with the presence of repeatability between tasks, some of the flies performed well in all the
332 tasks. The remaining studies involved social insects. Chittka et al. (2003) found that, across
333 different experiments, certain bumblebees consistently made rapid but imprecise foraging
334 decisions, whereas others took longer but achieved higher accuracy in their decisions. This
335 trade-off between speed and accuracy in foraging has been shown to be adaptive (Burns and
336 Dyer 2008; Muller and Chittka 2008) but it did not appear to apply to nestmate recognition in
337 wasps and ants (Baracchi et al. 2015; Baracchi et al. 2021). Muller and Chittka (2012) found
338 that some individual bumblebees learned better than other individuals in three types of
339 discrimination tasks (colour, shape, and odour), but Smith and Raine (2014) reported no
340 correlation between bumblebee performance across colour and odour discrimination learning
341 tasks. Finke and colleagues (2021) reported that some individual honey bees performed better
342 on visual tasks of varying complexity, suggesting a consistent aptitude for these types of
343 tasks. However, there was no correlation between performance in the visual task and the
344 equivalent olfactory task. Moreover, Finke and collaborators (2023) found a positive
345 correlation between an individual bee's ability to learn the simple discrimination task and
346 their performance in both reversal learning and negative patterning, suggesting that correlated
347 performance across learning paradigms is a distinct trait of honey bees. Interpreting the
348 discrepancies between the studies on bumblebees is currently challenging, and the differences
349 may be attributed, at least partially, to methodology. However, it seems reasonable to
350 conclude that individual differences across tasks are clearly present in certain species, such as
351 the honey bee. Last, in the European shore crab *Carcinus maenas*, a weak covariance
352 between learning and memory has been observed through a maze task, although it was not
353 attributed to consistent individual differences by the authors (Davies et al. 2019).

354

355 *Indirect evidence of individual differences*

356 From our research, it emerged that the invertebrate literature contains relatively few
357 studies that tested the repeatability of cognitive performance. One might conclude that
358 cognitive individual differences are less pronounced or less common in invertebrates than in
359 vertebrates. However, in this section, we present evidence that challenges this assumption:
360 additional invertebrate studies did not specifically test for repeatability, but their findings
361 support the presence of robust performance differences that are likely to be biological and
362 functionally relevant. A first set of relevant studies concerns cognitive performance and is
363 listed in Table 1. The species involved are mostly insects, but two species of cephalopods are
364 also included. The cognitive tasks investigated in insects are simple learning tasks. For
365 instance, Pamir and colleagues (2011) analysed a large data set (1640 subjects) of honey bees
366 tested with an olfactory conditioning task. They found that the group-average performance
367 was characterised by a progressively increasing learning curve. However, the learning curves
368 of individual subjects indicated rapid learning limited to short phases of the training. This
369 suggested the presence of individuality in learning performance. Similarly, in a reversal
370 learning task performed under the influence of the nectar alkaloid nicotine, Baracchi and
371 colleagues (2017) observed significant variability between individual bees in learning and,
372 thus, in terms of their response to nicotine and posited that this variability may be ascribed to
373 individual differences in susceptibility of learning to the alkaloid (Baracchi et al. 2017). The
374 two studies in cephalopods adopted more complex paradigms. Richter and colleagues (2016)
375 found systematic differences between seven octopuses trained on problem-solving tasks, such
376 as opening a container to retrieve a food reward. Huang and Chiao (2013) reported that some
377 individual cuttlefish, but not others, were able to learn a task by observing experienced
378 demonstrators.

379 Interestingly, two studies on bumblebees linked individual variation in learning tasks
380 to foraging performance in the field. Results from one study showed that bumblebees with

381 enhanced learning abilities foraged for fewer days than bumblebees with reduced learning
382 abilities (Evans et al. 2017). Conversely, the second study reported that individuals with
383 reduced learning had shorter foraging careers (Evans et al. 2021). It is not clear whether this
384 discrepancy is related to the two types of learning investigated (visual versus olfactory,
385 respectively). Notably, bumblebee colonies with higher learning abilities collected more
386 nectar than colonies with reduced learning abilities (Raine and Chittka 2008). This link
387 between individual cognitive differences and proxies of fitness has been reported several
388 times for vertebrates (e.g., Ashton et al. 2018; Cole et al. 2012; Huebner et al. 2019; Smith et
389 al. 2015). For the purposes of this review, the fact that individual cognitive differences are
390 linked to fitness components in invertebrates strengthens the hypothesis of their biological
391 significance.

392 A second set of studies, which indirectly supports the existence of individual
393 differences in invertebrate cognition, has focused on brain morphology. Van der Woude and
394 colleagues (2018) reported that brain size affects memory retention in the parasitic wasp
395 *Nasonia vitripennis* (although this effect was not detected in another parasitic wasp,
396 *Trichogramma evanescens*). Li and colleagues (2017) used whole-brain immunolabelling to
397 demonstrate that the density of synaptic complexes (microglomeruli) within the mushroom
398 bodies of the bumblebee brain was negatively correlated with learning and memory retention
399 in a visual discrimination task. These associations between cognitive variation and brain
400 morphology are common in vertebrates (e.g., Buechel et al. 2018; MacLean et al. 2014) and
401 support the idea of a biological basis for individual differences in cognition. Overall, this
402 literature containing indirect evidence suggests that solely considering repeatability
403 underestimates the existence of individual differences in invertebrates.

404

405 *Heritable individual differences*

406 The cognitive individual differences observed in vertebrates at the phenotypic level
407 are thought to be due in part to genetic variance (e.g., González et al. 2019; Gnanandesikan et
408 al. 2020; Langely et al. 2020; Smith et al. 2015) and in part to experiential factors, including
409 phenotypic plasticity (e.g., Ferrari 2014; Lucon-Xiccato et al. 2023). It is reasonable to
410 assume that the same may occur in invertebrates: heritability of performance on a cognitive
411 task in an invertebrate supports the presence of cognitive individual differences.

412 Heritability of cognitive functions has been extensively investigated in two
413 invertebrate models, the honey bee *Apis mellifera* and the fruit fly *D. melanogaster*. In the
414 honey bee, an early study estimated heritability values (h^2) of learning between 0.39 and 0.54
415 (Brandes et al. 1988). These values indicated that genetic differences can contribute up to
416 approximately half of the variation observed in the cognitive phenotype. More recent work
417 has focused on latent inhibition, which consists of ‘ignoring’ a stimulus that in the past was
418 not associated with consequences, resulting in a reduced ability to associate that stimulus
419 with a specific outcome. This learning trait is naturally variable in bumblebees. In several
420 studies, bumblebees were artificially selected for latent inhibition by controlled breeding of
421 queens and drones with similar latent inhibition abilities (Bennet et al. 2021; Cook et al.
422 2020; Lemanski et al. 2021; Sezen et al. 2021). The success of artificial selection implies a
423 significant heritability of the trait. Interestingly, bumblebees selected for enhanced inhibition
424 exhibited improved learning than controls. However, this improvement was observed only
425 when the learning tasks involved stimulation that engaged both the antennae and the
426 proboscis, rather than only the antennae (Sezen et al. 2021). Additionally, the artificial
427 selection also impacted foraging success (Cook et al. 2020; Lemanski et al. 2021), suggesting
428 a relationship between individual’s cognitive abilities and fitness.

429 The second major line of investigation on heritability involved the learning abilities of
430 fruit flies. Mery and Kawecki (2002; see also Kawecki and Mery 2006) exposed eight

431 populations of fruit flies to an experimental condition in which females could lay their eggs
432 in one of two available substrates with different mediums (e.g., A and B). In a first trial, one
433 of the two substrates (e.g., A) also contained quinine (an aversive tastant). Therefore, the flies
434 were expected to associate the presence of quinine with the A substrate, but not with the B
435 substrate. Subsequently, the flies were exposed again to the two substrates but without the
436 quinine. Here, flies that learned the association between substrate A and quinine were
437 expected to avoid the A substrate and lay their eggs in B. Only eggs laid in substrate B (i.e.,
438 the eggs of the flies that learned the association) were allowed to develop. After several
439 generations, the flies of this line showed an increased ability to avoid the substrate previously
440 associated with quinine, suggesting an evolution of learning ability. Research on these
441 artificially selected lines showed that the evolution of enhanced learning abilities came at the
442 cost of reduced competitive abilities at the larval stage (Mery and Kawecki 2003). Further
443 evidence supporting the heritability of cognition comes from a study on a *D. melanogaster*
444 line homozygous for one natural allelic variant at the foraging (*for*) locus (Mery et al. 2007).
445 The aforementioned study by Hollis and Kawecki (2014) also demonstrated the heritability of
446 cognitive abilities in fruit flies by detecting a correlated response to experimental evolution
447 for different levels of sexual selection. A response to experimental evolution for different
448 levels of sexual selection was also found in the seed beetle *Callosobruchus maculatus* with a
449 spatial chemosensory learning task (Baur et al. 2019).

450 A final example of the heritability of cognition was found in the parasitic wasp
451 *Cotesia glomerata*. In this species, a form of long-term memory is observed after a single
452 conditioning trial. Van den Berg and colleagues (2011) artificially selected a population of
453 wasps based on their ability to form long-term memories. This produced a line of wasps that
454 formed only a transitory memory (anaesthesia-sensitive memory) after a single conditioning
455 trial. Interestingly, a congeneric parasitic wasp *C. rubecula* showed only a form of short-term

456 memory, suggesting that selection based on natural individual differences can lead to
457 interspecific differences in mnemonic abilities. Last, evidence of heritability of the ability to
458 detect host cues was found in the parasitic wasp *N. vitripennis* (Koppik et al. 2015).

459

460 *Summary of evidence of cognitive individual differences*

461 Overall, based on the repeatability approach, there is limited evidence supporting the
462 presence of individual differences in cognitive abilities among invertebrates. It should be
463 noted that this approach may be problematic to apply to many invertebrate species due to
464 their short life span. If two measures are taken across different life stages and if trade-offs
465 between investment in cognition across stages exist, significant repeatability may be difficult
466 to detect. Using less restrictive inclusion criteria, the number of studies supporting the
467 existence of individual differences in invertebrates increases (Table 1). In line with the
468 vertebrate literature, we also found evidence for the heritability of cognitive differences in
469 invertebrates as well as evidence for a link with fitness. A limitation of invertebrate research
470 so far is that individual differences have been clearly shown in relatively few species (Fig. 3),
471 but with the advantage of an extensive knowledge about their behavioural ecology and
472 biology (e.g., fruit flies and Hymenoptera such as bees and bumblebees). Extending the
473 research to more species and higher clades will certainly increase the evidence of individual
474 differences. It is also worth considering the application of the formal repeatability approach
475 to studying individual differences that has been often applied to vertebrates. One finding that
476 deserves attention in future research is the existence of correlations between different tasks in
477 invertebrates, even when the tasks themselves are quite distinct. This may indicate the
478 presence of individual differences not only within specific cognitive abilities, but also of
479 covariation between different cognitive abilities, a well-known phenomenon in vertebrates
480 that is often associated with the presence of a general intelligence factor (e.g., Banerjee et al.

481 2019; Hopkins et al. 2014). A final noteworthy aspect is the abundance of artificial selection
482 studies in invertebrates. Conducting such studies is considerably more feasible in
483 invertebrates due to the lower costs associated with maintaining large populations and the
484 shorter generation time compared to vertebrates. The artificial selection approach in
485 invertebrates may also lead to understand more deeply trade-offs between cognition and other
486 traits. All these advantages make invertebrate models very useful for investigating cognitive
487 abilities and their evolution.

488

489 **Covariation with personality**

490 One hypothesis that has recently received substantial attention in vertebrate research
491 is that individual cognitive differences covary with consistent individual differences in
492 behavioural traits such as activity, boldness and sociability, the so-called animal personality
493 (Carere and Locurto 2011). For instance, it could be expected that more active individuals
494 would be hardwired to learn quickly because they encounter novel information at a higher
495 rate than less active individuals. The cognition-personality covariation hypothesis has
496 received considerable theoretical (Sih and Del Giudice 2012) and empirical support across
497 different vertebrate taxa (e.g., mammals: Brust and Guenther 2017; Mazza et al. 2018; birds:
498 Guillette et al. 2011; Medina-García et al. 2017; reptiles: Carazo et al. 2014; De Meester et al.
499 2022a; fish: Savaşçı et al. 2021; Trompt and Brown 2014). The covariance between cognition
500 and personality is particularly important in the context of cognitive variability. Individuals'
501 cognitive abilities positively affect fitness in many contexts (e.g., Cole et al. 2012; Smith et
502 al. 2015), so one would expect directional selection to reduce cognitive variability, unless
503 other forms of selection, trade-offs, or multiple trait selection are involved. Since a number of
504 studies have reported evolutionary explanations for variation in personality traits (Bergeron et
505 al. 2013; Dingemanse and Réale 2005; Le Coeur et al. 2015; Nicolaus et al. 2016), these

506 would likely favour cognitive variability via the indirect link between these two types of traits
507 (Lucon-Xiccato et al. 2020b), including cognitive sex differences (Lucon-Xiccato 2022).

508 The literature on cognition-personality covariation in invertebrates is growing in
509 parallel with the realization of the promising avenues offered by the study of invertebrate
510 personality (Kralj-Viser and Schuett 2014; Mather and Carere 2019; Mather and Logue
511 2013). Yet, it is still much less extensive than that available in vertebrates. Our review
512 highlights that insects appear to be the most promising taxonomic group for investigating this
513 topic (Table 2). This conclusion aligns with a recent meta-analysis that also examined the
514 association between personality traits and cognition, finding support for this association in
515 insects (Dougherty and Guillette 2018). Social insects are particularly informative because
516 they have evolved remarkable cognitive abilities including functional colony variation in
517 learning speed (Raine and Chittka 2008), and at the same time there is increasing evidence of
518 personality at the colony, caste, and individual level (e.g., Jandt et al. 2013, Perez et al. 2013;
519 Wray et al. 2011).

520 From the literature retrieved with our search (Table 2), three studies on ants revealed a
521 clear association between personality and cognitive traits. In carpenter ants (*Camponotus*
522 *aethiops*) consistent individual differences in exploratory activity were found to predict
523 learning performance. Active explorers were slower at learning than inactive explorers
524 (Udino et al. 2017). However, it is worth noting that Udino et al. (2017) also reported a lack
525 of personality-cognition covariation for two other behavioural traits in ants. In the same
526 species, differences in exploration tendency among individuals also predicted cognitive
527 judgement bias (d'Etorre et al. 2017). Finally, in *Aphenogaster senilis*, ants that exhibited a
528 higher tendency to explore their environment and responded more strongly to novel prey
529 items were more likely to use tools (Maàk et al. 2020). Interestingly, when tool-using ants
530 were removed, new tool-users could be predicted based on their personality scores.

531 Results comparable to those described for ants were found in two studies on crickets
532 (Table 2). In *G. texensis*, boldness, assessed through thigmotaxis behaviour, was correlated
533 with spatial learning abilities (Doria et al. 2019). Additionally, in *A. domesticus*, boldness
534 was correlated with olfactory discrimination learning (Albers and Reichert 2022). However,
535 two other behavioural traits measured in *A. domesticus*, namely neophobia and
536 aggressiveness, did not correlate with cognitive performance. It is worth noting that a recent
537 study by Beydizada et al. (2023) discovered a lack of correlation between boldness and a
538 basic form of learning, namely habituation, in *Menemerus semilimbatus*, a non-insect
539 arthropod. When spiders were tethered to a locomotor compensator, they displayed
540 habituation and dishabituation responses to visual stimuli projected on a screen. Moreover,
541 when tested in a shelter-equipped walking arena, they exhibited personality variations along a
542 shy-bold continuum. However, the habituation process was not influenced by individual
543 personality traits (Beydizada et al. 2023).

544 Two additional studies in insects from the list of Table 2 deserve special mention
545 because the cognitive traits investigated are directly related to the natural activities of the
546 species investigated. In the wasp *Polistes metricus*, the ability to recognise eggs introduced in
547 their nest by parasitic wasp was positively correlated with boldness and negatively correlated
548 with neophobia to olfactory stimuli (Wright et al. 2019). In the congeneric *P. dominula*, the
549 ability to recognise parasitic eggs was positively correlated with neophobia (Wright et al.
550 2019). A similar study has been performed in another phylum of invertebrates, the molluscs.
551 In cuttlefish *S. officinalis*, personality traits were correlated with measures of predatory
552 performance that could be attributed to cognitive traits such as attention (Zoratto et al. 2018).
553 The methodologies employed in these invertebrate studies clearly differ from the standard
554 paradigms of cognitive research typically used in vertebrates, such as discrimination learning
555 tasks. While these differences may pose challenges in directly comparing findings between

556 the two taxa, the fact that invertebrate studies often focus on natural-like cognitive tasks is
557 also a strength.

558

559 *Conclusions on cognition/personality covariance*

560 We found evidence of relevant research in invertebrates, but it was mostly limited to a
561 few insect species (Table 2). There are numerous promising invertebrate taxa that could be
562 further investigated to understand the links between personality and cognition. Cephalopods,
563 for instance, exhibit individual personality and possess remarkable cognitive abilities. Despite
564 extensive research on their cognitive abilities (e.g., Marini et al. 2017) the association
565 between personality and cognition in cephalopods remains largely unexplored, with only a
566 few studies touching upon the topic (e.g., Zoratto et al. 2018). Even within the insect group
567 itself, there is a vast potential for studying the correlation between personality and cognition.
568 In eusocial species, an interesting development of research on cognition/personality
569 covariation has been the analysis of group-level effects (e.g., Carere et al. 2018). Despite
570 these limitations, studies in invertebrate have provided insights, including what is probably
571 the first clear link between tool use and personality differences (Maak et al. 2020).
572 Invertebrate models might be particularly useful for addressing complex evolutionary
573 questions, such as the genetic basis of the covariation between personality and cognitive traits
574 that have implications for how behaviour and cognition evolves (e.g., independently or not).

575

576 **Caste differences**

577 One aspect of invertebrates that is likely to be important for the understanding of
578 cognitive variation, but it is lacking in vertebrates is caste differentiation. Caste
579 differentiation in social species involves the development of distinct morphological and
580 behavioural traits among individuals within the same species, resulting in individuals that

581 specialise in different tasks within the colony (Oster and Wilson 1978). Caste differences in
582 behaviour and morphology have been well studied (e.g., Jeanson and Weidenmüller 2014),
583 but less is known about caste differences in cognitive abilities. It is worth noting that these
584 caste differences may in part overlap with sex differences, which we discussed in the earlier
585 section of this review. In this section, we will focus on within-sex differences, specifically
586 among females, in different castes or subcastes within social insect colonies.

587 Cognitive demands can vary between castes because they have different reproductive
588 roles and tendencies towards specific tasks. In the paper wasp *Polistes dominula*, a
589 primitively eusocial species in which females are organised in a flexible caste system,
590 reproductive females had larger mushroom bodies (MBs) (centres of learning, memory and
591 sensory integration) than workers, as predicted by their sensory requirements for extensive
592 intra-colony interactions (Gandia et al. 2022). Similar trends have been found in highly
593 eusocial swarming wasps in the tribe Epiponini (O'Donnell et al. 2017), suggesting a link
594 between brain investment, social dominance, and castes. However, it is worth noting that in
595 other caste systems, such as that of termites, reproductive status was not associated with
596 increased investment in either antennal neuropils or MBs, suggesting that reproductive status
597 poses relatively little cognitive challenge (O'Donnell et al. 2022).

598 Studies on other social insects have also revealed caste-related differences in
599 cognitive abilities. Queens of both wild eusocial and parasitic bumblebee species were better
600 than workers at learning to associate a floral colour and nectar reward (Muth et al. 2021).
601 Similarly, queens of *Bombus terrestris* outperformed daughter foragers in visual
602 discrimination learning (Evans and Raine 2014), and young unmated *Apis mellifera* queens
603 showed better olfactory learning abilities than age-matched workers (Gong et al. 2018).
604 Finally, queens of *P. fuscatus*, a species of paper wasp with variable cuticular facial markings

605 that are used for social communication and individual recognition, were better than workers
606 at learning and remembering the faces of individual conspecifics (Tibbetts et al. 2018).

607 In honey bees, the worker caste system is based on age, with younger individuals
608 performing tasks such as brood care, queen care and nest building, while older individuals are
609 engaged in foraging and nest defence. Within the worker class, the age-based division of
610 labour results in subcaste-specific cognitive differences, as different tasks require different
611 cognitive abilities. Foraging activity in honey bees is linked to changes in the synaptic
612 boutons of MBs in their brains (Farris et al. 2001; Ismail et al. 2006; Withers et al. 1993).
613 Foragers have larger calyxes of MBs than nurse bees (Farris et al. 2001; Withers et al. 1993),
614 due to an increase in dendritic arbours and synaptic connections (Fahrbach et al. 1995; Farris
615 et al. 2001; Groh et al. 2012). Similar to honey bees, ants experience similar changes in brain
616 structure, with foraging associated with larger and more complex MBs than those in nest
617 workers (Gronenberg et al. 1996; Stieb et al. 2012).

618 In addition to differences in brain morphology, castes and subcastes in social insects
619 also differ in the titres of neurohormones and neuromodulators. In particular biogenic amines
620 play an important role in determining sub caste differences in cognitive abilities (Scheiner et
621 al. 2017). Division of labour among honey bee workers is achieved through variations in how
622 individual bees respond to stimuli that relate to particular tasks (Beshar and Fewell 2001).
623 For instance, young bees have a heightened sensitivity to sucrose and are more likely to
624 collect pollen or water in the future. On the other hand, bees with lower gustatory sensitivity
625 tend to collect only nectar (reviewed in Scheiner 2004). It is well known that gustatory
626 response-thresholds to sucrose can be affected by octopamine (OA) and its precursor
627 tyramine (Scheiner et al. 2002). Foragers have higher levels of tyramine in their brains and
628 show different mRNA expressions of a tyramine receptor in their brains than nurse bees.

629 Accordingly, foragers are better at sensing gustatory stimuli and had higher success rates than
630 nurses in appetitive learning and memory recall.

631 The adaptive value of differences in cognitive abilities among insect castes and
632 subcastes likely varies depending on the specific ecological and social context in which they
633 have evolved. A prevailing hypothesis for the adaptive value of caste-specific cognitive
634 abilities is that different castes have evolved to specialize in different tasks within the colony,
635 and that their cognitive abilities have evolved to support these specialized roles. Such
636 specialized cognitive abilities may allow castes to perform their tasks more efficiently and
637 effectively, ultimately benefiting the colony (Raine and Chittka 2008). Indeed, in social
638 groups, it may be advantageous to have individuals with varying cognitive abilities due to the
639 high energy cost of developing important learning and problem-solving skills. This has been
640 observed in bumblebee colonies, where some individuals make quick but inaccurate foraging
641 decisions, while others decide more slowly but with higher accuracy (Chittka et al., 2003;
642 Burns, 2005). The success of the colony benefits from having both highly skilled but costly
643 foragers and less accurate but cheaper animals, as this heterogeneity improves the
644 exploitation of different food sources and information distribution within the colony (Burns,
645 2005; Raine and Chittka, 2008). Cook et al. (2019) compared latent inhibition (LI), a non-
646 associative learning process that helps individuals to ignore familiar information in scouts
647 and recruits of honey bees and found that scouts, who encounter new odours while searching
648 for resources, had stronger LI than recruits who consistently forage from the same source.
649 This difference in learning ability may reflect the scouts' need to distinguish between high
650 and low-quality forage. Cook et al. (2019) also found that scouts had higher levels of
651 tyramine and octopamine than recruits, which may contribute to their better foraging skills.
652 Red wood ants (*Formica aquilonia*), which are characterized by huge colonies sizing up to a
653 million individuals and deep specialization, showed differences in aversive learning

654 depending on their task specialization (Iakovlev and Reznikova 2019). By contrast, in species
655 with small colony sizes such as *Temnothorax* species, specialists are no better at their tasks
656 than generalist workers (Dornhaus, 2008). In *Camponotus* ants, foragers possess a heightened
657 capacity to detect intruders compared to nurses and appear to have a greater inclination
658 towards attacking them (Larsen et al., 2016). This heightened sensitivity in foragers is
659 probably advantageous as younger workers usually remain in the nest and hardly come across
660 intruders. Having a sensitive recognition system would not be a useful trait for them and
661 would only add to the cost at the colony level.

662

663 *Summary of caste differences*

664 Overall, the existing literature suggests that caste-related differences in cognitive
665 abilities are common among social invertebrates and may be linked to the specific tasks and
666 roles that individuals perform within the colony. The adaptive value of caste-specific
667 cognitive abilities in social insects is likely to be context-dependent, as previously described
668 for similar behavioural variability (Jeanson and Weidenmüller 2014). Given the unique
669 characteristics of each social species and the presence of individual variation, including
670 tendencies and personalities, it can be challenging to make generalisations. A notable study
671 by Maak and collaborators (2020) exemplifies this complexity. The authors found that only a
672 few foragers within the worker class in an ant colony engage in tool use, and that this
673 behaviour is related to the personality of the individual worker. Therefore, the presence of
674 individual personalities within castes further adds to the complexity of apparently hard-wired
675 behaviours. Despite these challenges, exploring the fitness implications of cognitive variance
676 and cognition response to selective pressures through caste comparison holds considerable
677 potential to enhance our understanding beyond that from studies focused solely on vertebrate

678 species. It is encouraging to note that we already possess data concerning the potential
679 underlying mechanisms and substrates related to this aspect of cognitive variation.

680

681 **General conclusions**

682 Our literature search has highlighted that at least some invertebrate species and groups
683 exhibit all the forms of cognitive variation that have been described and are routinely
684 investigated in vertebrates, namely sex differences, individual differences, and correlations
685 between personality and cognition. The amount of evidence appears to be in rapid growth
686 (Fig. 4), with both practical and theoretical implications. From a practical standpoint, more
687 cognitive ecologists and researchers in other related fields should consider using invertebrate
688 species to answer questions concerning cognitive variation. On a theoretical level, the
689 parallelism observed between cognitive variance in vertebrates and invertebrates may
690 indicate that the evolutionary processes shaping cognition are fundamentally similar in both
691 groups. In other words, despite major differences in their nervous system, both vertebrates
692 and invertebrates exhibit convergent cognitive responses in terms of intraspecific variation
693 due to the selective pressure imposed upon them.

694 Several limitations in the existing invertebrate literature have been recognized,
695 especially in comparison to the extensive body of research available on vertebrates. First, we
696 need to broaden the number of species and taxa investigated in relation to cognitive variation.
697 Although we acknowledge that our literature search may have missed some of the existing
698 studies, there is a clear bias towards a few insect species, for instance Hymenoptera such as
699 bees and bumblebees (Fig. 2; Fig. 3). Other arthropods such as crustaceans and spiders, and
700 molluscs of the class Cephalopoda, which display complex cognitive abilities, are excellent
701 candidates for future research on intraspecific variability. Second, it is essential to diversify
702 the range of cognitive functions examined and move beyond a focus on relatively simple

703 forms of learning. For instance, sex-specific and caste-specific selection may act on highly
704 specialised forms of cognition rather than on general learning and memory functions. A
705 similar issue concerns the application of few standardised tasks to each species (e.g.,
706 olfactory discrimination in insects): at least between sexes and castes there may be sensory
707 differences (e.g., Bailey and Römer 1991; Willemart and Heberts, 2012) that affect the results
708 of cognitive tasks. By applying multiple paradigms to the same species, including some based
709 on different sensory modalities, it will be possible to disentangle the intraspecific variability
710 due to perception from that involving other cognitive domains. Third, it is important that
711 future research tries to adopt more closely some of the well-established approaches used in
712 vertebrates, such calculating repeatability to detect consistent individual differences.

713 As a future research direction, it is worth considering other forms of variance that
714 have not been directly addressed in this review. For instance, in vertebrate species, the
715 environment is known to have a pronounced effect on the cognitive phenotype due to
716 plasticity (e.g., Sauce et al. 2018; Lucon-Xiccato et al. 2023). Preliminary evidence suggests
717 that similar plasticity may occur in invertebrates (e.g., Black et al. 2018; Tsvetkov et al.
718 2019). Moreover, this cognitive plasticity is often related to stress responses (Lukowiak et al.
719 2014; Muth et al. 2015; Stefano et al. 2002; Templé and Richard 2015) and may be relevant
720 to animal responses to human-induced environmental change (Cabirol et al. 2023), including
721 for the evolution of novel traits (Badyaev 2005). Consistent with this idea, there is already
722 evidence of non-adaptive cognitive plasticity in invertebrate response to anthropogenic
723 stressors (Siviter and Muth 2022; Siviter et al. 2018). A final source of cognitive variability
724 that may be of interest for future studies is the age of individuals. In various vertebrates, age
725 has profound effects on cognitive abilities, both during development and senescence
726 (Chapagain et al. 2018; Gower and Lamberty 1993). In invertebrates, the study of aging

727 cognitive variability has not been undertaken so far, although it may be simplified by the
728 short life-span of many species.

729 Our review highlights that the study of cognitive variation in invertebrates offers
730 several advantages compared to vertebrate research, suggesting the importance of using the
731 two taxa as complements in future investigations. One notable advantage is the greater
732 feasibility of investigating the genetic basis of cognitive variation in invertebrates. In
733 particular, species such as the fruit fly and bumblebees have already provided a significant
734 amount of evidence regarding the genetic component of cognitive variation. The second
735 advantage lies in the study of eusocial insect species, which show marked biological
736 differences among individuals of different castes. This social organisation makes it possible
737 to formulate evolutionary hypotheses about what drives cognitive variation, including its
738 social component (Chittka and Rossi, 2022), and then, to test them by comparing well-
739 defined groups of individuals, a situation that in vertebrates is only possible for sex
740 differences. These advantages are currently underexploited. Once they are systematically
741 explored, many invertebrate taxa have the potential to become indispensable tools for
742 understanding the evolution of cognitive variation.

743

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1382 Table 1. Studies that provide indirect support for individual differences in the cognitive
 1383 performance of invertebrates, with detail on the species investigated and the cognitive task
 1384 adopted.

Species	Task	Study
<i>Apis mellifera</i>	Classical conditioning (odour)	Pamir et al. 2011
<i>Apis mellifera</i>	Classical conditioning (odour)	Pamir et al. 2014
<i>Apis mellifera</i>	Learning feeder location	Bar-Shai et al. 2011
<i>Bombus terrestris</i>	Classical conditioning (odour)	Smith and Raine 2014
<i>Bombus terrestris</i>	Classical conditioning (visual, colour)	Smith and Raine 2014
<i>Bombus terrestris</i>	Classical conditioning (odour)	Evans et al. 2017
<i>Bombus terrestris</i>	Classical conditioning (odour)	Evans et al. 2021
<i>Bombus terrestris audax</i>	Operant conditioning (visual, colour)	Baracchi et al. 2015
<i>Periplaneta americana</i>	Classical conditioning (visual, colour)	Arıcan et al. 2020
<i>Periplaneta americana</i>	Operant conditioning (spatial, T maze)	Arıcan et al. 2020
<i>Octopus vulgaris</i>	Problem solving	Richter et al. 2016
<i>Sepia pharaonis</i>	Social learning	Huang and Chiao 2013

1385 Table 2. Correlations between personality traits and cognitive traits in insects. The symbols
 1386 +, -, and NS indicate positive correlation, negative correlation, and no significant correlation,
 1387 respectively.

Species	Cognitive trait	Personality trait	Correlation	Study
<i>Aphaenogaster senilis</i> (ant)	Tool use	Exploration	+	Maák et al. 2020
<i>Camponotus aethiops</i> (ant)	Cognitive judgment bias	Exploration	- (considering optimistic bias)	d’Ettorre et al. 2017
<i>Camponotus aethiops</i> (ant)	Classical conditioning (olfactory)	Exploration	-	Udino et al. 2017
<i>Camponotus aethiops</i> (ant)	Classical conditioning (olfactory)	Sociability	NS	Udino et al. 2017
<i>Camponotus aethiops</i> (ant)	Classical conditioning (olfactory)	Aggressiveness	NS	Udino et al. 2017
<i>Gryllus texensis</i> (cricket)	Spatial learning (radial arm maze)	Boldness (thigmotaxis behaviour)	-	Doria et al. 2019
<i>Acheta domesticus</i> (cricket)	Discrimination learning (olfactory)	Boldness (thigmotaxis behaviour)	-	Albers and Reichert 2022

<i>Acheta domesticus</i> (cricket)	Discrimination learning (olfactory)	Aggressiveness	NS	Albers and Reichert 2022
<i>Acheta domesticus</i> (cricket)	Discrimination learning (olfactory)	Boldness (neophobia)	NS	Albers and Reichert 2022
<i>Nebria brevicollis</i> (beetle)	Associative learning (olfactory)	Boldness	NS	Harris et al. 2020
<i>Nebria brevicollis</i> (beetle)	Associative learning (olfactory)	Exploration	NS	Harris et al. 2020

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1389 **Figure captions**

1390 **Fig. 1** Conceptual framework illustrating the different forms of cognitive variation under
1391 investigation (sex differences, individual differences, personality differences, and caste
1392 differences) and their relationships. Cognitive sex differences in invertebrates are partly
1393 related to the caste differentiation in eusocial insects, although some caste distinctions are
1394 unrelated to sex. Cognitive variations that covary with personality are likely to represent
1395 specific forms of individual differences.

1396

1397 **Fig. 2** Taxonomic distribution of invertebrate species investigated for cognitive sex
1398 differences. The articles have been retrieved with keywords search and references/citation
1399 checking as described in the main text.

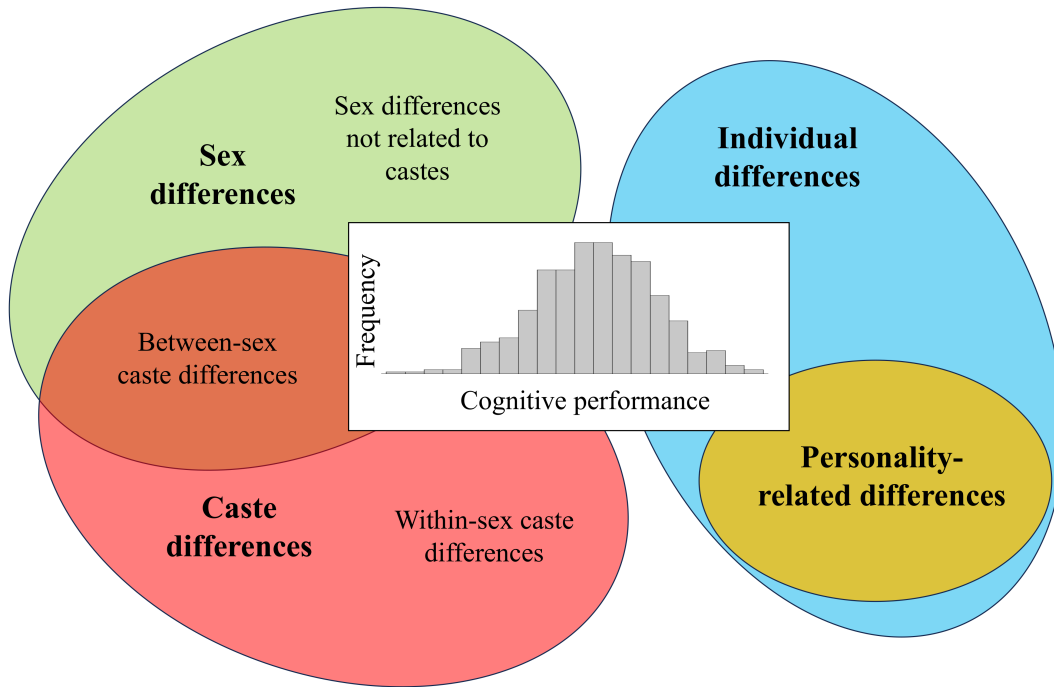
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1401 **Fig. 3** Taxonomic distribution of invertebrate species investigated for cognitive individual
1402 differences. The articles have been retrieved with keywords search and references/citation
1403 checking as described in the main text.

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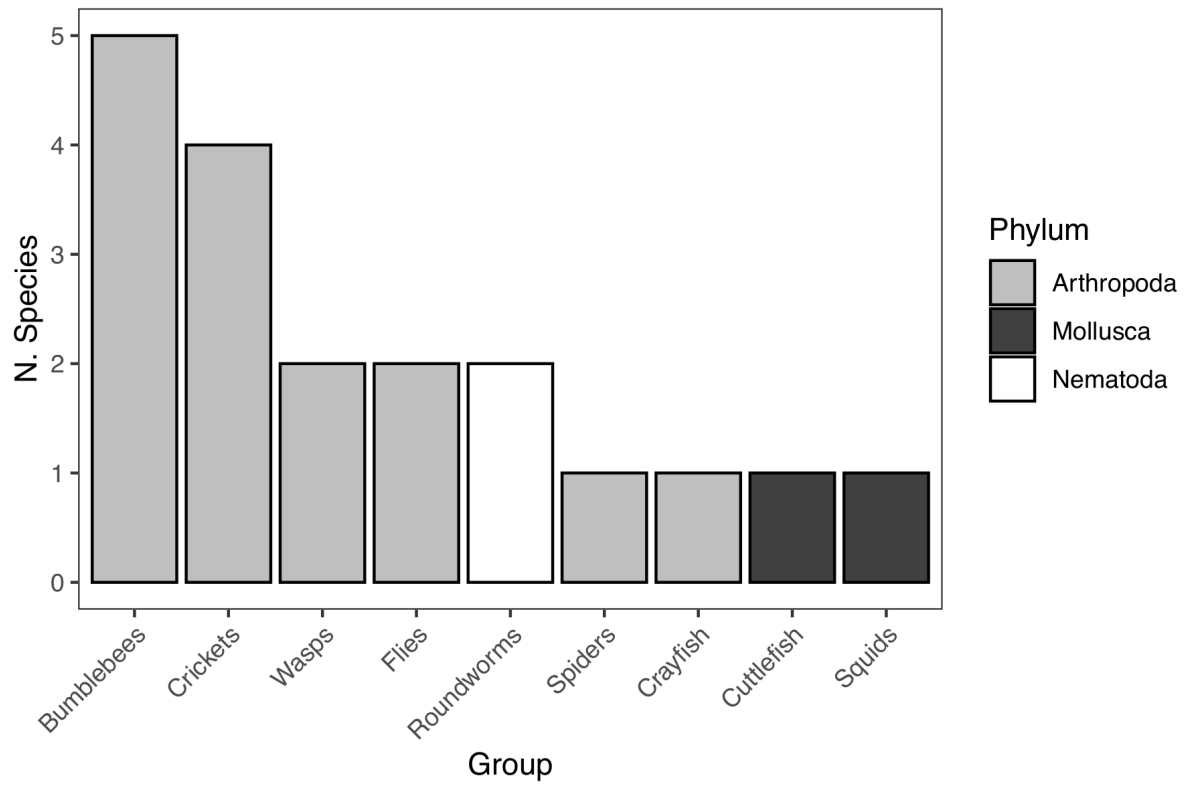
1405 **Fig. 4** Trend in the number of publications per year (left axis, red) and in the cumulative
1406 number of publication (right axis, blue) on variance in cognitive abilities of invertebrates.
1407 One earlier study published in 1988 and the studies published in 2023 are not included in the
1408 plot. The articles have been retrieved with keywords search and references/citation checking
1409 as described in the main text.

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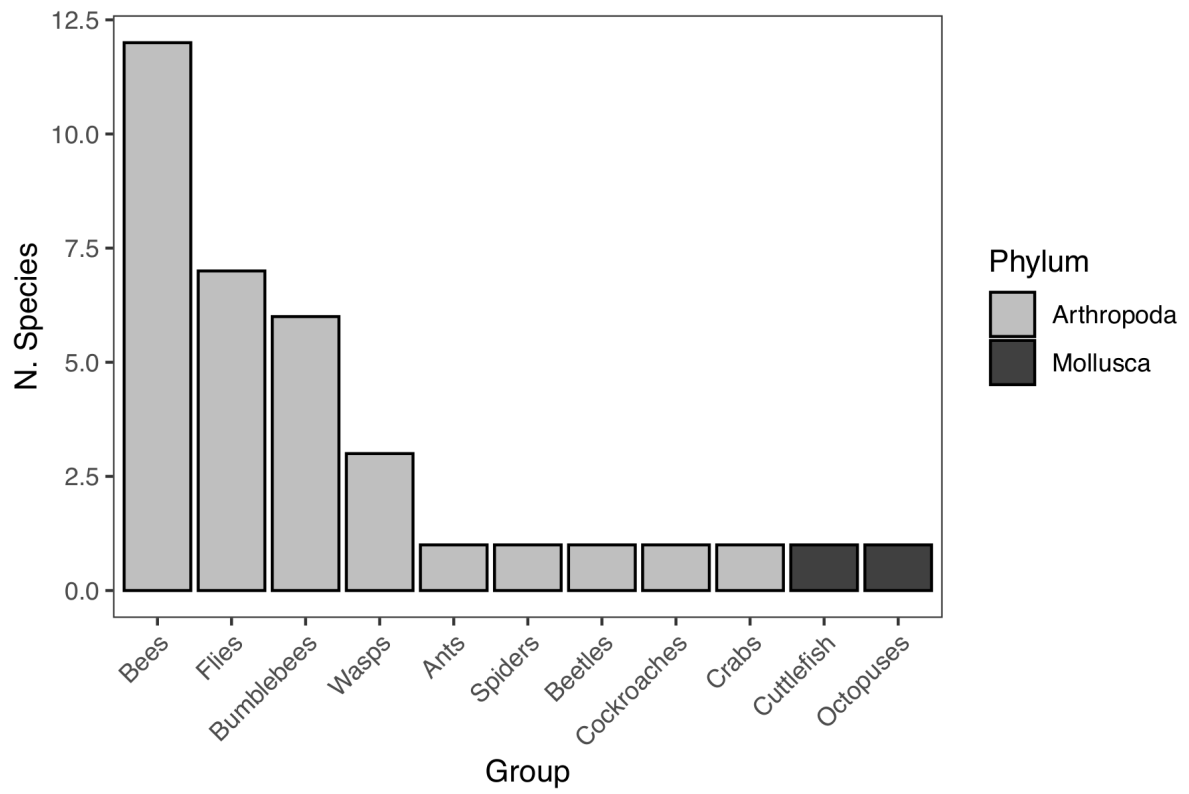
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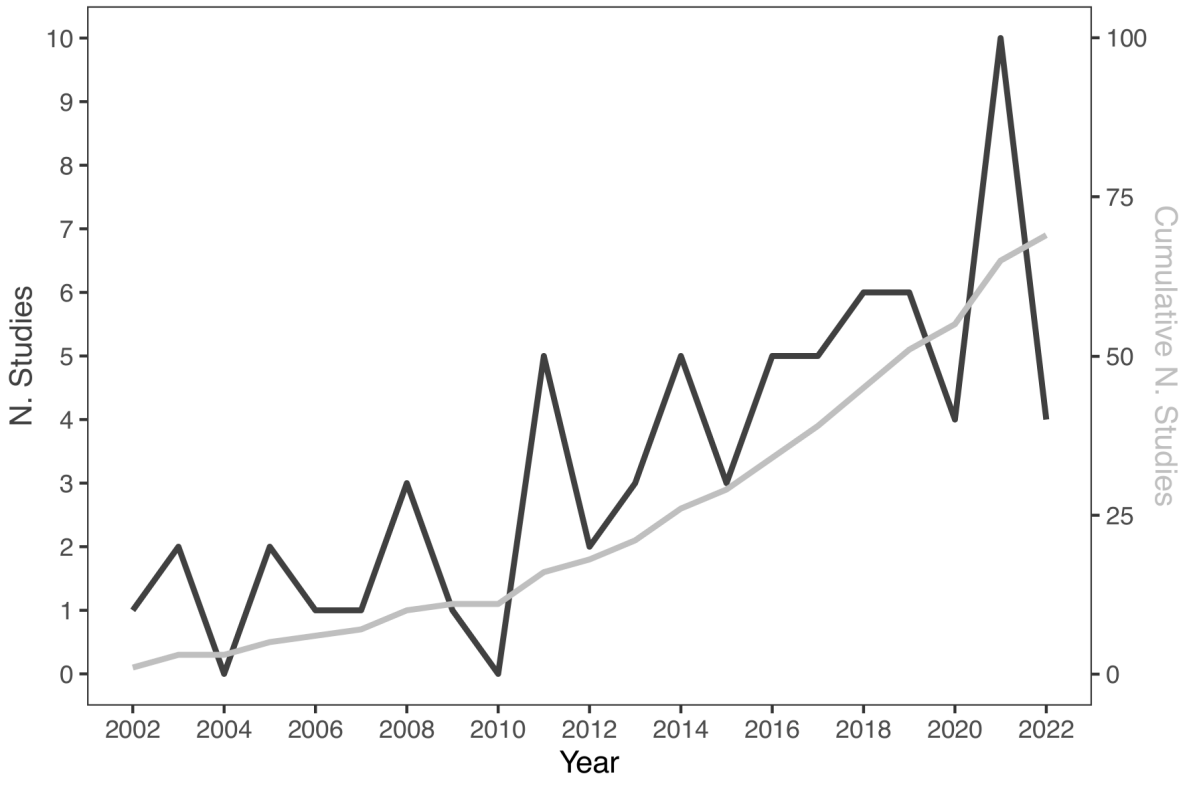
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