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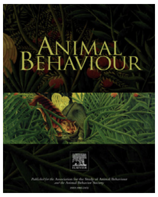

Differential effects of brain size on memory performance in parasitic wasps

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Small animals usually have relatively larger brains than large animals. This allometric brain–body size scaling is described by Haller's rule. However, one of the smallest known insects, *Trichogramma evanescens*, a parasitic wasp, shows brain isometry, leading to similar relative brain sizes in small and large conspecifics. The somewhat larger *Nasonia vitripennis* parasitic wasp displays diphasic brain–body size scaling with isometry in small individuals and allometry in large individuals. These two species may have undersized brains for small wasps, with reduced cognitive abilities. Here, we induced intraspecific body size variation in genetically identical *T. evanescens* and *N. vitripennis* and examined cognitive trade-offs of brain scaling. We compared visual and olfactory memory retention between small and large conspecifics. Results showed that diphasic brain scaling affected memory retention levels in *N. vitripennis*, whereas isometric brain scaling did not affect memory retention in *T. evanescens.* The two species may experience different evolutionary pressures that have shaped the cognitive consequences of isometric brain–body size scaling. A possible trade-off of brain isometry in *T. evanescens* could be present in brain properties other than memory performance. In contrast, it may be more adaptive for *N. vitripennis* to invest in other aspects of brain performance, at the cost of memory retention.

An individual's ability to learn and memorize has been related to the size of the brain, both absolute brain size and the size of the brain relative to total body size (Kotrschal et al., 2013; Roth & Dicke, 2005; Striedter, 2005). However, relative brain size also directly depends on body size: small animals have relatively larger brains than large animals. This is known as Haller's rule, and generally applies within and between animal species in all taxa (Gonda, Herczeg, & Merila, 2011; Harvey & Krebs, 1990; Isler et al., 2008; Kruska, 1996; Pagel & Harvey, 1989; Rensch, 1948; Riveros & Gronenberg, 2010; Seid, Castillo, & Wcislo, 2011; Stuermer et al., 2003; Wehner, Fukushi, & Isler, 2007). Haller's rule follows a power law function in which the exponent, the scaling coefficient, determines the shape of the relationship. The more the scaling coefficient approaches 0, the stronger the negative allometry that Haller's rule describes. A scaling coefficient that equals 1 describes a linear relationship known as isometry.

Allometric brain–body size scaling may be a consequence of several different mechanisms through which neural architecture determines behavioural output (Willemet, 2013). For instance, those neurons involved in regulation of somatic processes may be lower in numbers and in complexity of their neurites when body size is small. However, for those neurons involved in cognitive processes, which is not necessarily different between small and large animals, the absolute, not relative, number and size of neurons and connections determine the required neural processing power (Chittka & Niven, 2009). Small animals may thus need to form relatively larger brains to achieve similar levels of cognition as large animals.

This allometry implies that small animals suffer high energetic costs, because brain tissue has a high metabolic rate (Aiello & Wheeler, 1995). These energetic costs can become too high to be overcome by the smallest animals, which limits body miniaturization (Eberhard & Wcislo, 2011). Interestingly, some of the smallest insect species show unique intraspecific brain scaling properties, possibly to avoid the energetic costs of having a relatively large brain (see Groothuis & Smid, 2017 for a recent overview of brain scaling in differently sized insects). An example is shown by a species of polymorphic leaf-cutter ant, *Atta colombica*, individuals of which vary in body length between 5 and 10 mm

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(Feener, Lighton, & Bartholomew, 1988). Workers show an allometric relationship between brain and body size (Seid et al., 2011). However, a break point splits the allometry into two separate functions. Larger ants show a scaling coefficient of 0.29, which is comparable to scaling coefficients found for other ant species (Wehner et al., 2007). Smaller ants have a much larger scaling coefficient of 0.60.

Another example is given by a smaller species, the parasitic wasp *Nasonia vitripennis* (Fig. 1a). These wasps parasitize and develop inside fly puparia. Adult body size depends on the number of developing larvae inside the same host pupa because of scramble competition, resulting in body lengths of 1.2–2.4 mm measured from thorax to abdomen tip (Groothuis & Smid, 2017). Again, a break point divides the wasps into two groups where the smallest wasps have a larger scaling coefficient, which in this case is about 1, resulting in isometric brain–body size scaling (Fig. 2a).

The most extreme form of intraspecific brain scaling is shown by some of the smallest insects known, *Trichogramma evanescens* parasitic wasps (Fig. 1b). These minute wasps parasitize and develop inside lepidopteran eggs. Adult body size depends on scramble competition in a similar way as in *N. vitripennis*, resulting in body lengths of 0.3–0.9 mm (Van der Woude & Smid, 2016; Van der Woude, Smid, Chittka, & Huigens, 2013). *Trichogramma evanescens* wasps scale their brains isometrically with body size (Van der Woude et al., 2013; Fig. 2a). Small and large individuals of this species have the same relative brain size, with brains that are much smaller in the smallest *T. evanescens* and much larger in the largest *T. evanescens* compared to species with allometric brain–body size scaling.

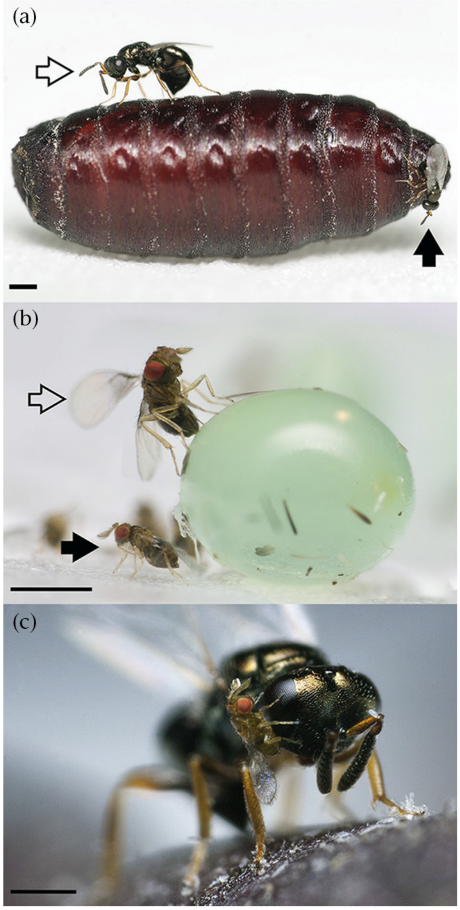

Figure 1. Phenotypic plasticity in body size, showing large (open arrows) and small (black arrows) wasps of the species used in this study: (a) *N. vitripennis* on a *C. vomitoria* host pupa; (b) *T. evanescens* on an *M. sexta* host egg; (c) a small *T. evanescens* on the head of a large *N. vitripennis*, illustrating the difference in body size between the two species. Scale bars indicate 0.5 mm. Photos: Jitte Groothuis.

The abovementioned examples show that isometric brain–body size scaling is observed in some of the smallest insects, possibly because small invertebrates avoid the excessive energetic costs that are associated with a relatively larger brain. A smaller relative brain size may enable smaller body sizes but may simultaneously cause trade-offs with brain performance when brains become too small to maintain all neural processing abilities. The smallest invertebrates could consequently show impaired learning abilities and reduced memory retention and suffer more from the metabolic costs that are associated with forming and retaining long-term memory (Hoedjes et al., 2011; Margulies, Tully, & Dubnau, 2005; Mery & Kawecki, 2005; Snell-Rood, Papaj, & Gronenberg, 2009). Notably, intraspecific allometry reflects the more limited developmental plasticity of brain size compared to body size in response to environmental constraints such as resource availability. Isometric brain–body size scaling may require a higher level of developmental plasticity of brain tissues than allometric brain–body size scaling and such developmental plasticity may evolve under specific constraints that occur in the smallest insects.

In the present study, we examined cognitive trade-offs of the developmental processes that underlie isometric brain–body size scaling that result in a small brain. We compared memory performance (level and duration of memory retention) of small and large conspecifics of *T. evanescens* and *N. vitripennis* (Fig. 1c), after both visual and olfactory conditioning. *Nasonia vitripennis* can form long-term memory of olfactory cues after a single experience of drilling a hole in the host pupa and feeding from its contents (Hoedjes & Smid, 2014; Schurmann et al., 2012). *Trichogramma evanescens* naturally hitchhike on mated female butterflies, which enables them to parasitize freshly laid eggs and form a long-term memory of the butterfly's antiaphrodisiac pheromone (Huigens et al., 2009; Kruidhof et al., 2012). Associative learning of colours is less frequently studied in these species, but has been described in both (Keasar, Ney-Nifle, & Mangel, 2000; Oliai & King, 2000).

We hypothesized that having a small brain compromises memory performance in small wasps of both species, because the observed isometry may be a result of a reduction in brain size beyond that required to maintain the same brain performance as larger conspecifics. We expected these effects to be more pronounced in *T. evanescens* than in *N. vitripennis*, because brain isometry is observed over the full size range in *T. evanescens*, which may be a consequence of more strongly miniaturized brains in small individuals than in *N. vitripennis*, where isometric–allometric brain–body size scaling was observed.

METHODS

Insects

Trichogramma evanescens (Hymenoptera: Trichogrammatidae) of inbred strain GD011 originating from a female collected near Wageningen, The Netherlands, were reared on UV-irradiated host eggs of the Mediterranean flour moth, *Ephestia kuehniella* (Lepidoptera: Pyralidae; obtained from Koppert Biological Systems, Berkel en Roderijs, The Netherlands; Huigens et al., 2009; Van der Woude et al., 2013). The wasps were kept in a climate room (22±1 °C, 50–70% relative humidity, 16:8 h light:dark), and used to create body size variants as described below.

Nasonia vitripennis (Hymenoptera: Pteromalidae) of inbred strain AsymCx, originating from a female collected in Leiden, The Netherlands (Breeuwer & Werren, 1995) were reared on *Calliphora*