

Quantity discrimination in *Tenebrio molitor*: evidence of numerosity discrimination in an invertebrate?

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Abstract Numerosity discrimination, the ability to distinguish between sets with more and less items, is recognised as the foundation for higher numerical abilities. Understanding numerosity discrimination from a comparative perspective is hence pivotal in tracing the evolution of numerical representation systems. However, numerosity discrimination has been well studied only in vertebrates, where two innate systems of number representation have been described: an ‘analog magnitude system’ used to discriminate among numerosities by representing them as cardinal magnitudes and a ‘parallel individualisation system’ that allows precise discrimination among small arrays of items (≤ 4) by representing objects individually. We investigated the existence of quantity discrimination in an insect species (*Tenebrio molitor*) by using a spontaneous two-choice procedure in which males were exposed to substrates bearing odours from different numbers of females (≤ 4) in increasing numerosity ratios (1:4, 1:3 and 1:2). We show that males can discriminate sources of odours reflecting 1 versus 4 and 1 versus 3 females, but not 2 versus 4 or 1 versus 2, indicating that *T. molitor* males exhibit a marked preference for sources reflecting more female donors only when numerosity ratios are below 1:2. We discuss the functional significance of this finding and whether our pattern of results could be best explained by

summation of a non-numerical continuous variable or by the existence of a numerosity discrimination mechanism with an operational signature ratio of 1:2.

Keywords Numerosity discrimination · *Tenebrio molitor* · Invertebrate · Chemical communication

Introduction

The study of numerical cognition is, from the existence of a concept of number to the arithmetic abilities of animals, among the topics that have aroused more interest within the field of comparative cognition (Roberts 1997; Dehaene 1997; Butterworth 1999; Bekoff et al. 2002). Complex mathematical abilities are founded on numerical representations and concepts—such as negative numbers, fractions or square roots—which are unique to language-based minds with the representational and combinatorial power of educated adult humans. However, there is growing evidence that higher numerical reasoning is rooted in innate numerical abilities that are widespread among vertebrates (Dehaene et al. 1998; Shettleworth 1998; Hauser 2000; Feigenson et al. 2004; Hauser and Spelke 2004). At the core of this suite of numerical abilities is ‘numerosity discrimination’: the ability to distinguish between two finite sets containing different amounts of items. The study of numerosity discrimination has become a cornerstone to understanding the evolution and distribution of number representation systems and numerical abilities in animals (Hauser and Spelke 2004).

So far, the available evidence suggests the existence of two innate numerosity discrimination mechanisms underlying two independent systems of number representation in vertebrates (Dehaene et al. 1998; Hauser 2000; Xu 2003;

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Uller et al. 2003; Feigenson et al. 2004; Hauser and Spelke 2004). The first mechanism is based on an ‘analog magnitude system’ that is used to discriminate between arrays of items by representing each set as an approximate cardinal magnitude. These representations exhibit scalar variability (Gallistel and Gelman 2000), are imprecise in that they only allow successful discrimination when the difference between two sets of items is above a certain ‘signature’ threshold (Dehaene et al. 1998; Feigenson et al. 2004; Hauser and Spelke 2004) and appear to follow Weber’s Law in that the discrimination between any two given sets is determined by the ratio between their represented magnitudes rather than by their absolute difference (i.e. numerosity ratio; Moyer and Landauer 1967). In contrast, the second mechanism is based on a ‘parallel individualisation system’ that functions by representing the different items in a set as individual objects or ‘object files’. Thus, individual objects are stored in working memory enabling precise discrimination by comparing the amount of objects in two sets on the basis of a one-to-one correspondence. Such discriminations are only possible as long as the amount of objects in both sets are within the operational limit of the system, which seems to be of three in human infants and four in non-human primates and other vertebrates (i.e. Trick and Pylyshyn 1994; Dehaene et al. 1998; Hauser 2000; Uller et al. 2003; Feigenson et al. 2004; Hauser and Spelke 2004; Barner et al. 2008).

Unfortunately, our knowledge and understanding of the origins and phylogenetic distribution of numerosity discrimination is largely restricted to vertebrates. Available comparative data include human infants (e.g. Wynn 1998; Xu 2003; Lipton and Spelke 2003), several mammals (e.g. Meck and Church 1983; Meck et al. 1985; Brannon and Terrace 2002; Hauser et al. 2000, 2003; Ferkin et al. 2005), a few birds (e.g. Honig and Stewart 1989; Roberts 1997; Pepperberg 2006; Rugani et al. 2007), a few fish species (Tegeger and Krause 1995; Agrillo and Dadda 2007; Agrillo et al. 2007; Buckingham et al. 2007) and one amphibian (Uller et al. 2003). That our knowledge about the numerical abilities of invertebrates is scant is, at least from an evolutionary perspective, perplexing. First, complex cognitive abilities have already been reported in numerous invertebrates (reviewed in Menzel et al. 2007) and previous studies hint at the existence of basic numerical abilities in at least some insect species (Chittka and Geiger 1995; Karban et al. 2000; Chen et al. 2003; Boisvert and Sherry 2006; Skorupski and Chittka 2006; Wittlinger et al. 2006; Dacke and Srinivasan 2008). Second, numerosity discrimination is bound to be highly adaptive in a wide range of contexts such as foraging (Farnsworth and Smolinski 2006), social group formation (Tegeger and Krause 1995) and competition (McComb et al. 1994), antipredator tactics (relying on group number; Beauchamp

2003), avoidance of conspecific brood parasitism (Lyon 2003) or sperm competition (Thomas & Simmons 2009). Indeed, most of the functional contexts that are thought to provide the selective pressure for the evolution of numerosity discrimination abilities in vertebrates are also found in invertebrates. Moreover, some invertebrates have evolved in specific functional contexts that seem to require some kind of numerosity discrimination ability. For example, the ability to assess the risk and/or the intensity of sperm competition (e.g. through the assessment of competitor density and/or sex ratios at the time of mating) has been reported in several insect species (e.g. Carazo et al. 2007; Thomas and Simmons 2009) and seems to depend on the existence of some kind of numerosity discrimination mechanism.

Particularly suggestive is the case of the yellow mealworm beetle (*Tenebrio molitor*). *T. molitor* is a highly polygynandrous beetle that has evolved several strategies in response to an evolutionary history of intense sperm competition (e.g. Happ 1969; Drnevich et al. 2000; Griffith 2001; Drnevich 2003; Carazo et al. 2004). For example, when remating takes place at short intervals, males of *T. molitor* are capable of preventing sperm release from the spermatophore of a rival male (i.e. spermatophore inhibition), achieving near complete sperm precedence (Drnevich et al. 2000). As a counter-strategy, males use chemical cues to assess approximate male abundance at the time of mating, a cue to immediate sperm competition risk and intensity levels, and accordingly adjust the amount of time they allocate to guarding their spermatophore (Carazo et al. 2007). Thus, the available evidence suggests that male beetles use chemical cues to assess approximate male/female abundance at the time of mating, an ability that hints at the existence of some kind of numerosity discrimination mechanism.

Almost all of the studies that have investigated numerosity discrimination in vertebrates have been conducted using visual or auditory stimuli (e.g. Dehaene et al. 1998; Hauser 2000; Feigenson et al. 2004). However, chemical signals mediate individual recognition in many species (Thom and Hurst 2004), including insects (e.g. D’Ettorre and Heinze 2005) and there are thus theoretical reasons to expect that chemicals could mediate numerosity discrimination in contexts where visual and auditory cues are absent or in species, such as *T. molitor*, in which chemicals represent the main avenue for communication (Wyatt 2003; Carazo et al. 2004). In fact, numerosity discrimination based on chemical cues has recently been reported in meadow voles (Ferkin et al. 2005) and a recent experiment suggests that crickets (*Teleogryllus oceanicus*) are capable of assessing the approximate number of male individual signature odours left in a female during mating (Thomas and Simmons 2009).

Here, we investigated the existence of quantity discrimination in *T. molitor* by using a spontaneous two-choice procedure in which males were exposed to substrates bearing odours of different numbers of females (≤ 4) in increasing numerosity ratios (1:4, 1:3 and 1:2). Males of this species are attracted to substrates bearing female sex-pheromones and we expected that, if males are able to discriminate between two sources of odours reflecting different numbers of female donors, males should exhibit a preference towards the source reflecting more female donors (Tschinkel et al. 1967; Tanaka et al. 1986; Happ 1969; Happ and Wheeler 1969; Carazo et al. 2004).

Methods

All the beetles used in this study originated from stock cultures maintained in our laboratory. These cultures have been running for more than 10 years with regular contributions from other cultures. All growth stages are kept together in plastic trays with a rearing medium consisting of white flour and wheat bran to which chunks of fruit, bread and various vegetables are added periodically. The culture is covered with filter paper that is sprayed with water for moisture on a daily basis. All containers are kept in well-ventilated, dark storage cabinets, at ambient humidity and under temperature-controlled conditions.

Subjects used in our experiments were collected from the stock cultures and sexed as pupae by inspection of developing genitalia on the ventral side of the eighth abdominal segment (Bhattacharya et al. 1970). Individuals were examined under a dissecting microscope both as pupae and after eclosion and those with obvious malformations were discarded. Sexed adults of the same age were kept separately in plastic containers measuring approximately 15 (height) \times 13 \times 20 cm until used in the experiments. Plastic containers were conditioned and maintained in the same way as stock cultures. Odour donor and experimental beetles were virgin, sexually mature (i.e. at least 10 days post-eclosion) and never older than 30 days. Trials were conducted at a temperature of 22–25°C, at ambient humidity and under dim red lighting.

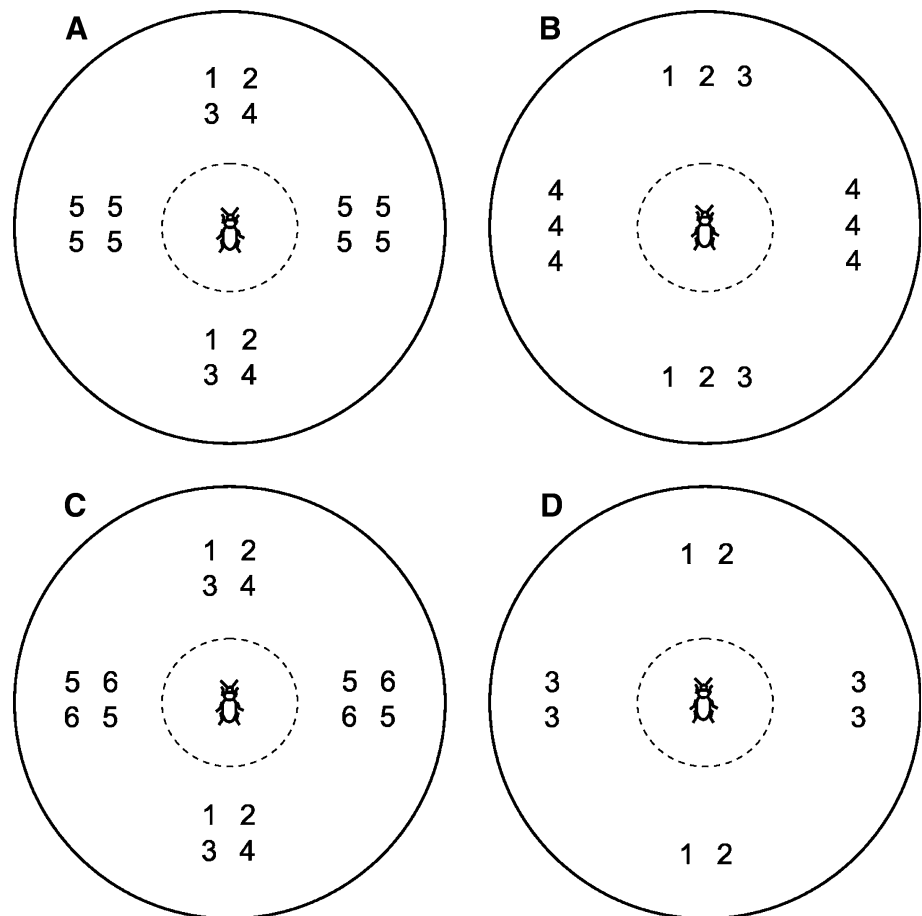
To investigate the ability to discriminate between chemical cues reflecting different numbers of donor females, we haphazardly assigned experimental males to one of four treatment groups and exposed all the beetles in each group to one of the following combinations of odour cues representing increasing numerosity ratios: (a) odour cues from 1 versus 4 donor females, (b) odour cues from 1 versus 3 donor females, (c) odour cues from 2 versus 4 donor females and (d) odour cues from 2 versus 1 donor

female. Each experimental male participated in only one trial.

Odours were collected by placing each donor female in a plastic petri dish measuring 5 cm in diameter and lined with white filter paper for the 24 h immediately preceding each trial (Carazo et al. 2007). All females were thoroughly examined for injuries and weighted to the nearest 0.1 mg. To control for non-numerical attributes (i.e. the quantity and quality of pheromones left by each female), all donor females used in the same preference test had the same reproductive and nutritional status (see Rantala et al. 2003; Carazo et al. 2004), approximately the same age (± 5 days; Happ 1969) and were selected so that the maximum mass difference allowed was 3 mg, representing approximately 2% of the mean weight of female donors ($\bar{x} \pm \text{SEM} = 126 \pm 1.6$ mg). Females acted as odour donors in more than one test (i.e. either 2 or 4 tests) but their odours were alternated so that they acted as donors for the two odour sources composing each preference test. For example, females donating odours in a 1 versus 4 versus test acted as donors both for the source reflecting four females and for the source reflecting one female. Furthermore, sources of odours from different donor females were arranged so that chemicals from different females did not overlap and were encountered by experimental males sequentially.

Trials were run in a circular arena consisting of a 19 cm diameter glass dish inverted over a 21 \times 26 cm piece of white filter paper (Worden et al. 2000; Carazo et al. 2004). Immediately preceding trials, filter papers from each donor female were cut into 1 cm² pieces that were placed equidistant from each other and from the centre of the arena according to the pattern illustrated in Fig. 1. Males were placed in the centre of the arena and restrained under a 5 cm diameter plastic petri dish for 5 min. Following this acclimation period, the plastic dish restraining the male was removed. Trials began as soon as the experimental male had visited both sources of odours and lasted 10 min during which we used a blind protocol to record the time the male spent in contact with each odour source (Carazo et al. 2004). Briefly, to ensure the observer conducting behavioural recordings was unaware of the composition (i.e. number of marking females) of each of the odour sources comprising each trial, a different researcher set up the experimental arena and coded the odour sources. A few males spent most of the time immobile in the centre of the arena so tests in which experimental males spent less than 60 s inspecting odour sources were discarded from the analyses. As we could not assume that data were normally distributed, we conducted the Wilcoxon signed ranks test for paired replicates (Siegel and Castellan 1989) to test for male preference for odour sources reflecting more female donors. All reported *P* values are two-tailed.

Fig. 1 Diagram showing the experimental layout used to test the response of male beetles to pieces of filter paper bearing odour cues from female odour donors in **a** 1 versus 4 experiments, **b** 1 versus 3 experiments, **c** 2 versus 4 experiments and **d** 1 versus 2 experiments. Each *number* represents a different 1 cm² piece of filter paper. *Different numbers* indicate different female odour donors within each trial. *Dotted circles* represent small petri dishes used to restrain the experimental male during the 5 min acclimation period preceding trials



Results

Male beetles, *T. molitor*, spent significantly more time inspecting filter papers bearing odours from four females than inspecting filter papers bearing odours from one female (1 vs. 4 test, $n = 33$, $z = 2.78$, $P = 0.005$) and spent more time inspecting filter papers bearing odours from three females than inspecting filter papers bearing odours from one female (1 vs. 3 test, $n = 35$, $z = 2.72$, $P = 0.007$). In contrast, males did not differ in the amount of time they devoted to inspecting paper cues bearing odours from 2 versus 4 ($n = 34$, $z = 1.12$, $P = 0.262$) or 1 versus 2 ($n = 30$, $z = -0.051$, $P = 0.960$) females (Fig. 2). All P values that are reported as significant remained so after applying Holm's (1979) sequential Bonferroni correction for experiment-wise error rate due to multiple testing.

Discussion

Male *T. molitor* beetles 'go for more'

Our results show that *T. molitor* males discriminate between odour sources reflecting different numbers of

donor females in spontaneous two-choice tests in which experimental subjects are given the choice between odours from 1 versus 4 or 1 versus 3 female donors (Fig. 2). In particular, and as predicted, males were more attracted to odour sources with odours from more donor females. Similar results (i.e. where discriminating individuals 'go for more') have been reported in two-choice tests investigating numerosity discrimination in other species, in different biological contexts (e.g. Uller et al. 2003; Hauser et al. 2003; Agrillo and Dadda 2007). That *T. molitor* males are more attracted to sources reflecting more females agrees with theoretical expectations arising from the reproductive system of this species (Drnevich et al. 2000; Drnevich 2003) and may be adaptive in at least two ways. First, *T. molitor* exhibits a polygynandrous mating system where females mate multiply (with the same or different males) at short time intervals (Drnevich et al. 2000; Drnevich 2003), so odour cues reflecting more females are likely to represent greater reproductive opportunities for males. Second, the ability to assess female densities, together with previous results that show that males can assess approximate male densities at the time of mating (Carazo et al. 2007), may allow males to estimate the sex ratio at different locations and select those with lower

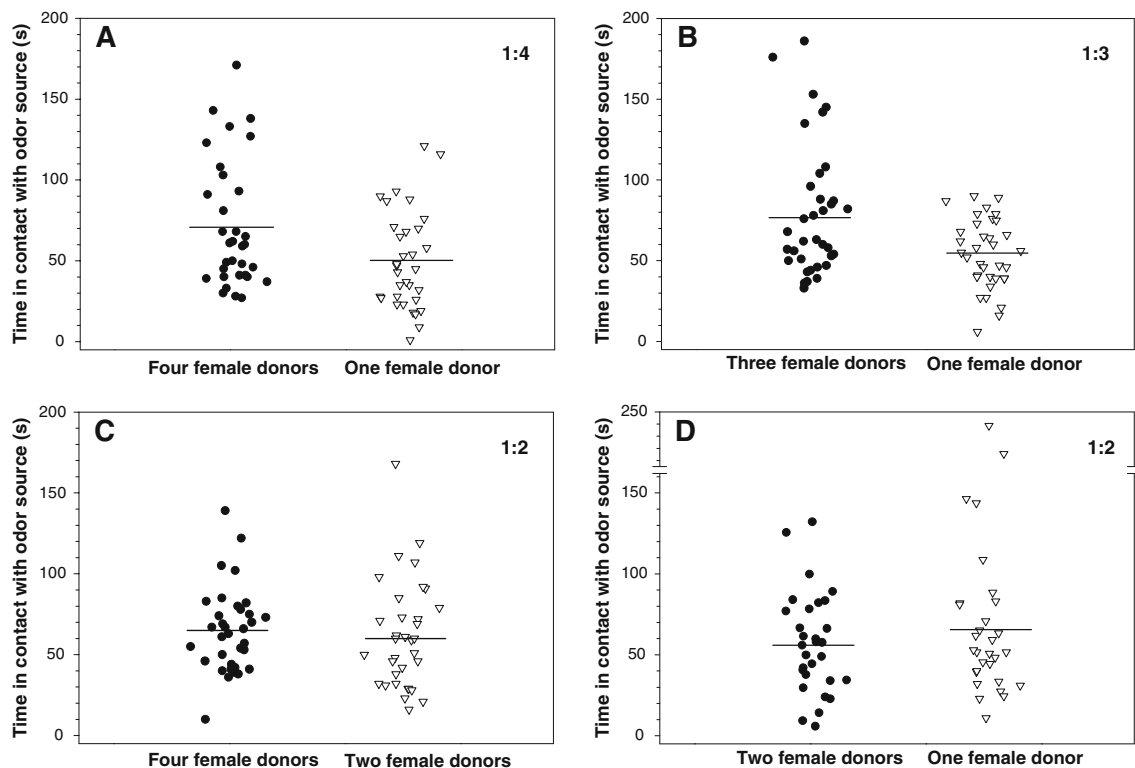


Fig. 2 Total time that males spent in contact with each type of odour source during 10 min trials in: **a** 1 versus 4 experiments ($n = 33$), **b** 1 versus 3 experiments ($n = 35$), **c** 2 versus 4 experiments ($n = 34$) and **d** 1 versus 2 experiments ($n = 30$). Graphs show all the data points for each test. To display multiple data points with the same numerical

value, we moved the locations of symbols by adding noise to the x coordinate of each data point. Noise was generated from a uniform distribution on a small interval centred on zero (Cleveland 1993). Horizontal lines represent α -Windsorized mean values ($\alpha = 0.5$)

sperm competition levels, a crucial determinant of the reproductive output in this species.

Rudiments of number in insects?

Previous studies have suggested that at least some insect species may be able to estimate countable quantities (Chittka and Geiger 1995; Karban et al. 2000; Chen et al. 2003; Boisvert and Sherry 2006; Skorupski and Chittka 2006). Particularly suggestive is recent evidence on desert ants (*Cataglyphis fortis*), that apparently use some sort of step integrator or ‘step counter’ to evaluate distances during path integration (Wittlinger et al. 2006) and honey bees (*Apis mellifera*), that seem able to count landmarks when navigating in search of food sources (Dacke and Srinivasan 2008). However, the debate is open whether at least some of the former studies present evidence of numerosity discrimination or whether, conversely, quantity discrimination is based on summation of a continuous variable (Franks et al. 2006). Summation of a continuous variable that correlates with numerosity can be used to estimate a countable quantity without directly assessing numerosity, in the same way that an odometer estimates distance without actually ‘counting’ kilometres (Franks et al. 2006).

Thus, the major hurdle in proving numerosity discrimination lies in convincingly demonstrating that quantity discrimination cannot be explained in terms of the summation of a continuous variable.

Of the non-numerical or continuous variables that may correlate with the number of donor females in an odour source, the most obvious is the amount or intensity of chemical compounds making up each source. Although the specific chemical compounds upon which the discrimination is based are unknown (but see Carazo et al. 2004), we used donor females of the same age, reproductive status, size and condition, all of which may affect the quality and/or quantity of female odours (Happ 1969; Brown 1990; Rantala et al. 2003; Carazo et al. 2004). Second, we carefully controlled the time female donors were left to mark filter paper subsequently used in trials (Rantala et al. 2003) and the total amount of marked filter paper (i.e. total area and number of pieces of filter paper) making up each odour source (Fig. 1). Thus, although different odour sources corresponded to different numbers of donor females, both the quality and the total amount of chemical cues in each odour source were randomized across trials, making it very unlikely that the observed differences in male behaviour were due to differences in the quantity (i.e.

scent mark intensity, area or number of filter papers) or quality (i.e. hedonistic value of donor females) of the chemicals in each odour source (see also Thomas and Simmons 2009). Another possibility is that males are monitoring the complexity of the mixture of chemical compounds making up each odour source and are simply more attracted to odour sources with a higher diversity of chemical elements in the mixture. However, the available evidence from behavioural and chemical studies suggests that the chemical compounds underlying fine-grained discrimination in *T. molitor* are non-volatile (Griffith 2001). Consequently, our experimental setup was designed so that the different individual odours composing each source were encountered sequentially, hence constituting temporally distinct events and reducing the probability that odour sources are perceived as a mixture. If the different odours composing a given odour source are not perceived simultaneously (i.e. as a mixture), then the amount of chemical compounds processed at any given instant will not differ according to the numerosity of the odour source because males will only perceive one odour at a time. Still, it could be argued that male beetles are spending more time in odour sources with scents from more females simply as a by-product of the need to process a larger amount of different odours. Three lines of evidence argue against this possibility. First, *T. molitor* beetles are seemingly capable of assessing subtle differences in female scents extremely rapidly (e.g. Carazo et al. 2004). Second, this hypothesis would fail to explain why we did not find differences in exploration time in trials where males were given the choice between odour sources from 2 versus 4 and 1 versus 2 female donors. Finally, and perhaps most conclusive, is the fact that the time males spent inspecting different odour sources does not seem to depend on the number of donor females composing each odour source, but rather on the combination of the odour sources in each particular trial.

Needless to say, this does not mean that beetles are not using the chemical diversity of an odour source to evaluate numerosity. For example, males could be using a sequential ‘accumulator model’ to tally the number of chemical elements composing a source in a sequential manner. Thus, if a given odour source is composed by four different odours (i.e. pertaining to four different females) males could accumulate the total number of different elements in the source sequentially, as they explore the four different odours and construct an analog magnitude to be compared to those constructed while processing other sources of odours (Hauser 2000). Meck and Church’s (1983; Meck et al. 1985) pioneer experiments suggest that rats use a very similar model both for timing (i.e. ‘Scalar Expectancy Theory’ model of timing) and to discriminate between different numerosities. Unfortunately, this is but one of several different numerosity mechanisms that males could

be using and, with little or no information about how chemical stimuli are processed in this species, any discussion about putative underlying mechanisms is merely speculative (Chittka and Brockmann 2005).

In short, the results presented show that, at least when small arrays of donors are involved (≤ 4), *T. molitor* males are capable of chemically discriminating between two sources of odours according to the number of female donors contributing to each source. While we cannot rule out the possibility that this pattern of results may be explained in terms of the summation of an unknown non-numerical variable, we suggest our results fit nicely with the existence of a numerosity discrimination mechanism in this species (e.g. based on chemical identity signatures; Thom and Hurst 2004). Interestingly, while males of *T. molitor* discriminated between odour sources reflecting numerosity ratios of 1:4 and 1:3, they consistently failed to discriminate between odour sources reflecting a numerosity ratio of 1:2 even in the apparently simple task involving 1 versus 2 females. These results suggest that *T. molitor* would not be using a ‘parallel individualisation system’ but a different system that allows them to discriminate groups with different numbers of items (i.e. female donors) only when the ratio between the numerosities in each group exceeds 1:2. From a theoretical point of view, it could be argued that this high signature ratio is not reflecting a limit intrinsic to the ‘representational system’, but a functionally significant threshold. However, the available evidence points in the opposite direction, predicting that *T. molitor* males should be sensitive to subtle changes in female sex-pheromones or in female density (Happ 1969; Happ and Wheeler 1969; Gage and Baker 1991; Drnevich et al. 2000; Drnevich 2003; Carazo et al. 2004, 2007).

In our view, numerical cognition studies with invertebrates are usually met with much greater skepticism than studies with vertebrates despite the fact that the same criticisms can often be levelled against work with these two animal groups. There are few single experiments that can conclusively dismiss an interpretation in terms of the subjects’ monitoring of some non-numerical magnitude in an analogue way. Perhaps the best proof of numerosity discrimination comes from a few vertebrate species where cumulative results arising from a wealth of studies using diverse experimental approaches provide convincing evidence of numerosity discrimination (e.g. Feigenson et al. 2004; Hauser and Spelke 2004). Therefore, the key to prove the existence of numerosity discrimination in invertebrates is to provide results, on several fronts, that are most consistent with the existence of such a mechanism. We believe our results sum up with recent evidence (Chittka and Geiger 1995; Karban et al. 2000; Chen et al. 2003; Boisvert and Sherry 2006; Skorupski and Chittka 2006; Wittlinger et al. 2006; Dacke and Srinivasan 2008)

to suggest the existence of numerosity discrimination in at least some insect species and hope they will stimulate further research that may confirm or reject this hypothesis in *T. molitor*. The study of numerical cognition in invertebrates is crucial to answer questions with far reaching evolutionary consequences relative to the origin and evolution of numerical cognition in human and non-human animals and should in the future attract much more attention than it has done in the past.

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