

# *Nephila clavipes* spiders (Araneae: Nephilidae) keep track of captured prey counts: testing for a sense of numerosity in an orb-weaver

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**Abstract** *Nephila clavipes* golden orb-web spiders accumulate prey larders on their webs and search for them if they are removed from their web. Spiders that lose larger larders (i.e., spiders that lose larders consisting of more prey items) search for longer intervals, indicating that the spiders form memories of the size of the prey larders they have accumulated, and use those memories to regulate recovery efforts when the larders are pilfered. Here, we ask whether the spiders represent prey counts (i.e., numerosity) or a continuous integration of prey quantity (mass) in their memories. We manipulated larder sizes in treatments that varied in either prey size or prey numbers but were equivalent in total prey quantity (mass). We then removed the larders to elicit searching and used the spiders' searching behavior as an assay of their representations in memory. Searching increased with prey quantity (larder size) and did so more steeply with higher prey counts than with single prey of larger sizes. Thus, *Nephila* spiders seem to track prey quantity in two ways, but to attend more to prey numerosity. We discuss alternatives for continuous accumulator mechanisms that remain to be tested against the numerosity hypothesis, and the evolutionary and

adaptive significance of evidence suggestive of numerosity in a sit-and-wait invertebrate predator.

**Keywords** Cognitive ecology · Counting · Food hoarding · *Nephila* · Web spider

## Introduction

Many animals keep track of the number of items they encounter in their daily lives without language-based arithmetic. Instead, they possess an innate ability to approximate counts and represent them in memory, a “sense of numerosity” (Dehaene 1997; Brannon and Cantlon 2009; Shettleworth 2010). The sense of numerosity has been widely reported in vertebrates, including birds, fish, lions, hyenas, primates, racoons, and rodents (McComb et al. 1994; Dehaene 1997; Gallistel and Gelman 2000; Wilson et al. 2001; Brannon and Roitman 2003; Hauser et al. 2003; Ferkin et al. 2005; Pepperberg 2006; Buckingham et al. 2007; Agrillo et al. 2008; Beran 2008; Burr and Ross 2008; Cantlon and Brannon 2006; Kitchen and Beehner 2007; Brannon and Cantlon 2009; Shettleworth 2010; Bensom-Amram et al. 2011; Bogale et al. 2011; Scarf et al. 2011; Schmitt and Fischer 2011; Jones et al. 2014). Numerosity has also been reported in much smaller animals with very different body plans and brain configurations, including ants, bees, beetles, and jumping spiders (Dacke and Srinivasan 2008; Carazo et al. 2009; Bar-Shai et al. 2011; Reznikova and Ryabko 2011; Nelson and Jackson 2012).

The widespread taxonomic distribution of the sense of numerosity, together with the diversity in the life history of the animals that possess it, suggests that it is an ancient trait representing a basic feature of animal brains, large and

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small. But we have relatively little information about how the sense of numerosity varies with the ecology and life style of different species. This hampers our ability to test adaptive hypotheses about the evolution of numerosity, although it is clear that animals use it in crucial activities such as aggression, group formation, and foraging (McComb et al. 1994; Wilson et al. 2002; Buckingham et al. 2007; Agrillo et al. 2008; Dacke and Srinivasan 2008; Shettleworth 2010; Bar-Shai et al. 2011; Bensom-Amram et al. 2011; Reznikova and Ryabko 2011; Nelson and Jackson 2012). To gain a better understanding of whether and how the sense of numerosity varies among animals, it will be necessary to complement standard task-training experimental paradigms with methods whereby the natural behavior of animals helps reveal the features of their environments and experiences that are represented in their minds (Healy and Rowe 2010; Reznikova and Ryabko 2011; Schmitt and Fischer 2011).

Here, we use a field experiment to probe memory contents and test hypotheses about the sense of numerosity in a sit-and-wait invertebrate predator, *Nephila clavipes* golden orb-web spiders. Two features of the natural history and behavior of these spiders allowed us to conduct experiments with them as we found them in the field, using their natural reactions to prey capture and removal. First, *N. clavipes* accumulate prey larders on their web (Robinson and Mirick 1971; Rodríguez et al. 2013). After capturing a prey item, these spiders bring the prey to the hub of their web and secure it there with a silk line before feeding on it (except for very small prey, which they simply hold in their mouthparts). If at this point another prey is snared by the web, the spiders interrupt feeding to capture and secure the new prey to the hub. They may thus accumulate a larder at the hub of their web, with each prey item hanging by a single silk line (Fig. 1; Online Resource 1). Note that these larders differ from the “rubbish bands” accumulated by other *Nephila* species, which may include plant matter, may have additional functions besides food storage, and

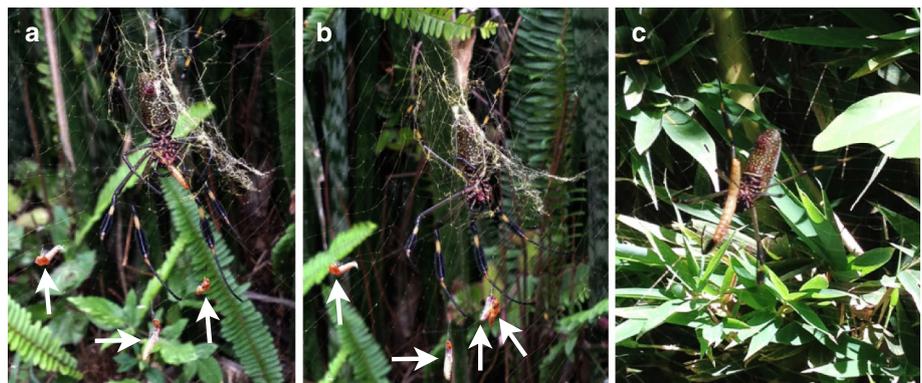
are located outside the hub of the web (Champion de Crespigny et al. 2001; Griffiths et al. 2003; Bjorkman-Chiswell et al. 2004).

The second feature of *N. clavipes* behavior that facilitated this experiment is that these spiders search for prey that has been removed from their web. In nature, *N. clavipes* mainly lose prey to kleptoparasitic *Argyrodes* spiders (Araneae: Theridiidae) (Robinson and Mirick 1971; Rypstra 1981). However, their searching behavior can also be elicited by any change in the location of prey on the web (e.g., by wind; Rodríguez et al. 2013), and it can be elicited by experimental removal of prey (Rodríguez and Gamboa 2000; Rodríguez et al. 2013). *Nephila clavipes* that are searching for lost prey explore their web by moving about it and out to the web frame, forcefully tugging on the web lines (Online Resource 2). This behavior differs from how they normally react when an object falls on their web; i.e., with quick directed approaches and tugging (Rodríguez and Gamboa 2000; Rodríguez et al. 2013).

The behavior of searching for lost items provides a convenient and natural assay of the prey features that are represented in spider memory. This assay has been used to demonstrate memory of web landmarks and of items on the web in *N. clavipes* and other web spiders (Baltzer 1924; LeGuelte 1969; Rodríguez and Gamboa 2000; Opell 2001; Rodríguez and Gloudeman 2011; Rodríguez et al. 2013). In particular, *N. clavipes* form memories that include some measure of the quantity of captured prey, and they use those representations to regulate searching efforts when the prey are removed from their web: These spiders search for longer intervals when they have lost larger individual prey items, as well as when they have lost larders consisting of more prey items (Rodríguez and Gamboa 2000; Rodríguez et al. 2013).

Our goal in this paper was to elucidate how the quantity of prey is represented in the memory of *N. clavipes* (henceforth, *Nephila*). We tested two hypotheses. (1) *Nephila* represent the number of prey that they have captured—i.e., they possess a sense of numerosity. (2) *Nephila*

**Fig. 1** *Nephila clavipes* accumulate prey larders at the hub of their web. **a** One spider has accumulated three prey items (arrows), each hanging from the hub, and is wrapping a fourth prey item, which she is holding in its mouthparts. **b** The same spider, now with a four-prey larder (arrows). **c** Another spider, wrapping one large prey item



represent an integration or accumulation of a continuous variable that correlates with prey numbers (Franks et al. 2006). For hypothesis (2), we focus on total accumulated prey mass. However, there are other possibilities for continuous variables to influence the representation of the number of captured prey that remain unaddressed by this experiment (see “Discussion”). Both hypotheses predict that search times will increase with the quantity of lost prey (Rodríguez and Gamboa 2000; Rodríguez et al. 2013). However, they may be distinguished if there are differences in the rate of increase in search times as a function of prey numbers versus prey size. We tested for such differences with an experimental manipulation of the composition of the prey larders accumulated by *Nephila*. We varied either the size of single prey items, or the number of prey items of the same size. Spiders thus accumulated equivalent prey quantities (mass) in treatments of prey numbers or prey size. We then probed spider memory contents by monitoring the searching behavior elicited by removal of the prey from the web and asked if searching increased more steeply with the size or the number of lost prey items.

Prior work has rejected the hypothesis that searching for lost prey does not reflect memory of prey features, but is instead prompted by remaining cues on the web, or by hunger or motivation (Rodríguez and Gamboa 2000; Rodríguez et al. 2013). We replicated tests of this hypothesis to confirm prior findings that point to memory as a key regulator of searching behavior. First, we tested for an artifact arising from our experimental procedure of prey removal. If this procedure elicits searching (rather than memory of the prey), then sham prey removal should produce searching. Prior work has rejected this prediction for *Nephila* (Rodríguez and Gamboa 2000; Rodríguez et al. 2013). Here, we repeated this test with a small sample size because of its confirmatory nature. The remaining confirmatory tests involved our experimental spiders and thus have larger sample sizes. Second, we assessed the effect of encountering plant debris or remnants of old prey on the web. If searching is not regulated by memory, searching spiders that encounter plant debris or old prey remnants on their webs should cease searching. By contrast, if such

spiders resume searching, it would indicate that they recognize the difference between the debris and the searched-for prey, implicating memory in their ability to make the distinction. The latter has been found to be the case in prior work with *Nephila* (Rodríguez and Gamboa 2000; Rodríguez et al. 2013). Finally, we tested for a potential role of motivation (rather than memory) in influencing search times. If searching reflects differences in the spiders' motivation, then behavior indicative of motivation should vary among our experimental treatments in parallel with searching behavior. We used the time it takes spiders to return to the hub of their web after experimental prey removal (before searching) as an assay of motivation (Rodríguez et al. 2013). We expect longer return times to represent negative influences on motivation (e.g., due to disturbance during the experimental procedure). By contrast, we expect shorter return times to represent positive influences on motivation (e.g., due to greater hunger, greater stimulation, or greater silk expenditure with larger prey larders). Note that return times may also be influenced by memory, but differences between the patterns for return and search times allow distinguishing the effects of memory and motivation (Rodríguez et al. 2013). Similarly, if searching is influenced by motivation, return times and search times should be inversely correlated.

## Methods

We conducted the experiments during December 2013 and January 2014 near San Rafael de Heredia, Heredia Province, Costa Rica (10°01'0225"N 84°06'45.24"O, elevation 1,227 m).

We tested for differences in the rate of increase in search times as a function of prey numbers versus prey size with two different experiments: a prey-count experiment and a prey-size experiment. Treatments in the prey-count experiment consisted of allowing spiders to accumulate larders of either one, two or four small prey, and then removing the entire larder. Treatments in the prey-size experiment consisted of allowing spiders to form larders of

**Table 1** Manipulation of the size of prey larders accumulated by *Nephila clavipes* spiders, varying the number of prey of equal size or the size of single prey items

Larder size treatment	Method of manipulating larder size	
	Varying prey counts; each prey item: mass = $27 \pm 1$ mg (mean $\pm$ 1 SE)	Varying the size of single prey items
1	1 prey ( $n = 8$ spiders)	1 small prey, mass = $27 \pm 1$ mg ( $n = 7$ spiders)
2	2 prey ( $n = 12$ spiders)	1 medium prey, mass = $49 \pm 4.6$ mg ( $n = 13$ spiders)
4	4 prey ( $n = 11$ spiders)	1 large prey, mass = $103 \pm 4.2$ mg ( $n = 14$ spiders)

one single prey item of either small, intermediate or large size, and then removing the prey (Table 1). Prey sizes were such that one large item was equal in mass to four small items, and one intermediate item was equal to two small items (Table 1; Fig. 1). We standardized prey taste, smell, and palatability using commercially acquired mealworm larvae (*Tenebrio molitor*; Coleoptera: Tenebrionidae) of different sizes (instars). Mealworms are not natural prey for *Nephila* (Robinson and Mirick 1971; Nentwig 1985; pers. obs.), but were readily accepted by the spiders. We haphazardly assigned each spider to one treatment in one of the experiments. In total, we tested 68 adult female spiders (including the control trials, see below), using each individual only once.

To begin a trial, we lightly dropped a larva on the sticky spiral of the spider's web. We allowed the spider to perform its normal prey capture behavior with each prey item (locate prey, extract it from sticky spiral, bring it to the hub, wrap it in silk, and secure it to the hub) and to settle into feeding for 30 s. For the treatments of two and four prey items, we repeated this procedure to reach the desired larder size.

Before removing the prey to elicit searching behavior, we induced the spider to retreat to the web frame by lightly touching her on the abdomen and legs with a scissors. Spiders varied in the disturbance required to induce them to retreat, and we categorized them as “easy” (a single contact or a few) or “difficult” (several touches required over several seconds) to induce to retreat. We then cut the silk line attaching the prey to the hub. Note that this procedure leaves the web intact, and it leaves no remnant of the removed prey.

We then timed with a chronometer how long spiders took to return to the hub after prey removal, and how long they searched for. We ended observations when spiders had remained immobile at the hub for 3 min, which prior work shows is a reliable indication that the spider will not resume searching (Rodríguez et al. 2013).

To confirm prior work indicating that searching for lost prey reflects memory of prey features, we first replicated a control experiment with a sham procedure in which we induced spiders that had no prey to retreat from the web as above. We then monitored the behavior of those spiders. Because this control only confirms prior results with identical methods (Rodríguez and Gamboa 2000; Rodríguez et al. 2013), we only tested a small sample of spiders ( $n = 3$ ). We also monitored the searching behavior of experimental spiders that had plant debris or old prey remnants on their web, seeking evidence that encountering such items might modify or end their searching. Finally, we related the time it took individual spiders to return to the hub after prey removal (return times) and their search times in two different ways: We compared the patterns of these

two measures among treatments, and we tested for a correlation between the two measures.

### Statistical analysis

We conducted all tests in JMP v. 7.0.1 (SAS Institute, Cary, NC, USA). We used models with either search times or return times as the dependent variable. There was heteroscedasticity for search and return times in the prey-size experiment (Levene's test;  $F \leq 0.055$ ) but not the prey-count experiment ( $F \geq 0.13$ ). We thus used General Linear Models (normal distribution, link identity function) for significance testing. We asked whether search and return times increased with larder size, and we asked whether such increase differed among experiments (prey counts vs. size). We used a model that included the following independent variables: larder size; experiment (prey count vs. size); and the larder size  $\times$  experiment interaction. The interaction term represents the test for a difference in the rate of increase in search times with prey numbers versus prey size. The model also included a covariate coding for whether the spider had been “easy” or “difficult” to induce to retreat from the hub before removing its prey (see above).

In addition to significance testing of the interaction term in the above model, we compared the effect size (Nakagawa and Cuthill 2007) of the interaction term (difference in rate of increase in search times with prey numbers vs. prey size) with the effect size of the increase in search times with prey numbers or prey size. We calculated effect sizes ( $r$ ) from the  $P$  value of the corresponding tests, thus:

$$r = Z/\sqrt{n}$$

where  $Z$  is the standard normal deviate equivalent of the  $P$  value and  $n$  is the sample size of the test (Rosenthal 1994).

For the effect of prey number and prey size, we included not only information from the present study but also from prior work that first reported these effects (Rodríguez and Gamboa 2000; Rodríguez et al. 2013). This allowed us to compare the effect size of the interaction term (difference in the rate of increase in search times with prey numbers vs. prey size) with the mean weighted effect size of the increase in search times with prey numbers or prey sizes, as well as to assess the replicability of findings as they accumulate (cf. Braver et al. 2014). To this end, we weighted effect sizes by the sample size to approximate expected variance in the effect size estimates (Shadish and Haddock 1994). We transformed  $r$  estimates to  $Z$  with Fisher's transformation (Sokal and Rohlf 1995), thus:

$$Z = 0.5 \ln[(1 + r)/(1 - r)] = \tanh^{-1}(r)$$

We then weighted  $Z$  by the parameter  $W = n - 3$  and calculated the weighted transformed mean effect size thus:

$$Z_r = (\sum W_i Z_i) / \sum W_i$$

Finally, we back transformed to  $r$  thus:

$$r = \tanh(Z_r)$$

We also assessed the robustness of the interaction term with Akaike's Information Criterion. We obtained AIC values for models with and without the interaction, favoring the model with the lower AIC value. To base model comparison on the amount of unexplained residual variation, we calculated AIC values from the standard least squares implementation of the models, thus:

$$AIC = 2K + n \ln(RSS/n)$$

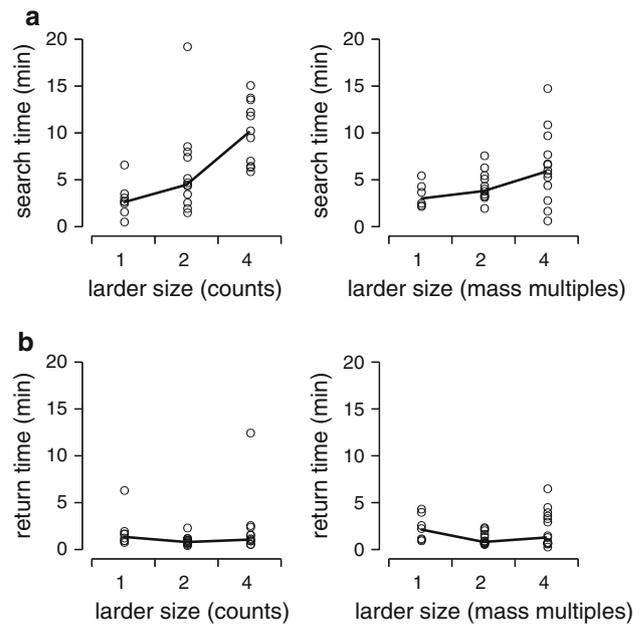
where  $K$  is the number of terms in the model;  $n$  is the sample size; and RSS is the residual sum of squares (Burnham and Andersson 2002).

We assessed the relationship between return and search times with Pearson's product-moment correlation.

## Results

All 31 spiders in the prey-numbers experiment searched for lost prey larders, as did 31 of 34 (91 %) spiders in the prey-size experiment (Online Resource 2).

Search times increased with larder size in both experiments (prey-count experiment:  $\chi^2_1 = 14.99$ ,  $P = 0.0001$ ; prey-size experiment:  $\chi^2_1 = 6.27$ ,  $P = 0.012$ ). Search times approximately doubled with each doubling of the number of prey in a larder, but increased by only 30–50 % with each doubling of prey mass (Fig. 2a). Thus, the effect size of prey counts was greater ( $r = 0.68$ ) than the effect size of prey size ( $r = 0.41$ ). This is consistent with prior work, where search times also approximately doubled with prey counts (Rodríguez et al. 2013; effect size:  $r = 0.58$ ) but increased only by 38 % with a near doubling of prey length (Rodríguez and Gamboa 2000; effect size:  $r = 0.18$  in a test that was nonsignificant, although with  $n = 13$  this was likely due to low statistical power). Across these prior studies and the present paper, the mean weighted effect size was  $r = 0.65$  for prey numbers and  $r = 0.36$  for prey size. Thus, a difference in the rate of increase in search times with prey numbers versus prey size seems to be a robust finding. Accordingly, in the present study, the increase in search times was steeper in the prey-count experiment than in the prey-size experiment, as indicated by the significant larder size  $\times$  experiment interaction (Table 2). Although the  $P$ -value for this interaction was relatively high and its effect size relatively low ( $r = 0.22$ ),



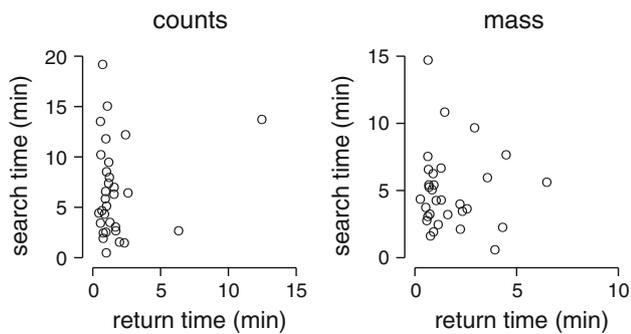
**Fig. 2** *Nephila clavipes* behavior after experimental removal of prey larders varying in size either as a function of prey counts or of the size of single prey. **a** Spiders searched longer for larger larders in both experiments. However, the increase in search times was steeper in the prey-count experiment (left versus right panels). **b** Return times did not vary with larder size. Lines indicate median values

**Table 2** Variation in the behavior of *Nephila clavipes* spiders that captured and lost prey larders consisting either of varying numbers of prey of the same size (prey-count experiment) or single prey items varying in size (prey-size experiment)

Variation in search time	$\chi^2_1, P$
Experiment (prey count vs. prey size)	<b>6.20, 0.013</b>
Larder size	<b>20.67, &lt;0.0001</b>
Experiment $\times$ larder size	<b>4.23, 0.04</b>
Difficulty to induce to retreat	0.42, 0.52
Variation in return time	
Experiment (prey count vs. prey size)	0.07, 0.80
Larder size	1.11, 0.29
Experiment $\times$ larder size	0.10, 0.75
Difficulty to induce to retreat	0.000002, 0.99

We tested for differences in search and return times (see text). The main purpose of these tests was to ask whether there was a difference between the two experiments in the rate of change in search and return times with larder size. Thus, the key term in the analysis is the experiment  $\times$  larder size interaction. We show the other terms for completeness. The term for experiment tests for overall differences in search and return times between experiments. It is significant for search times because the steeper increase in the prey-count experiment (see Fig. 2a) means that on average search times were higher in this experiment. The term for larder size tests for overall increases in search or return times with larder size across experiments

Significant terms are indicated in bold



**Fig. 3** No correlation between *Nephila clavipes* return and search times after experimental removal of prey from their web. This was the case regardless of whether larder size was varied with prey counts (left;  $r = 0.16$ ,  $P = 0.40$ ,  $n = 31$ ) or with the size of a single prey item (right;  $r = -0.04$ ,  $P = 0.82$ ,  $n = 31$ ). Pooling all data the lack of correlation held ( $r = -0.10$ ,  $P = 0.46$ ,  $n = 62$ )

there is support for the relevance of this term. Comparing AIC values for models with and without the interaction term,  $\Delta\text{AIC}$  was 2.23 in favor of the model with the interaction. Note also that the analysis was influenced by an outlier in the 2-prey count treatment (Fig. 2a left panel). Removing the outlier strengthened the interaction ( $\chi^2_1 = 7.13$ ,  $P = 0.008$ ;  $\Delta\text{AIC} = 5.25$  in favor of the model with the interaction; effect size:  $r = 0.31$ ).

By contrast, return times did not vary with larder size in either experiment (prey-count experiment:  $\chi^2_1 = 0.51$ ,  $P = 0.48$ ; prey-size experiment:  $\chi^2_1 = 0.69$ ,  $P = 0.41$ ) (Fig. 2b), and the larder size  $\times$  experiment interaction was nonsignificant (Table 2). Also, there was no correlation between return times and search times (Fig. 3).

The term coding for whether spiders were easy or difficult to induce to retreat from the hub before prey removal was never significant (Table 2).

The results of the control trials confirmed prior work (Rodríguez and Gamboa 2000; Rodríguez et al. 2013). Sham prey removal failed to elicit searching. Further, in several trials ( $n = 29$ ), spiders had plant debris or old prey remnants on their web. In all such cases, spiders came across and examined the debris or remnants during searching (with two spiders taking the remnants in their mouthparts) but resumed searching right away.

## Discussion

*Nephila clavipes* spiders accumulate prey larders on their webs and search when the prey are removed: *Nephila* search longer when they have lost larders that contained more prey items, as well as when they have lost larger single prey items (Rodríguez and Gamboa 2000; Rodríguez et al. 2013; this study). This searching behavior reflects the representation of prey features in memory: It is not an

artifact of our experimental procedure; it is linked to prey loss; it is robust to distractions such as the presence on the web of debris or prey remnants; and it is not confounded by hunger or motivation (Rodríguez and Gamboa 2000; Rodríguez et al. 2013; this study). Thus, *Nephila* form memories of prey they have accumulated and use those memories to regulate recovery efforts when the larders are pilfered.

We asked about the representation of prey quantity (numerosity vs. an integration of mass) in *Nephila* memory. We manipulated prey quantity in treatments of prey counts versus size. We found that searching increased both with prey counts and size, but did so more steeply with counts. We interpret these results as indicating that *Nephila* track both prey numerosity and size and that they give more weight to prey numerosity in the regulation of searching efforts. In other words, we find tentative support for the hypothesis that *Nephila* spiders possess a sense of numerosity, in addition to their ability to form representations of overall prey quantity or size. The difference in the steepness of the increase in search times as a function of prey counts versus prey size that we find is consistent with stronger effects of prey counts versus size in prior work (Rodríguez and Gamboa 2000; Rodríguez et al. 2013), but we caution that this test should be replicated for confirmation. An additional caveat is that, besides prey mass, other continuous variables may influence the representation of the number of captured prey. Indeed, neural mechanisms that represent counts may involve continuous accumulators (Gallistel and Gelman 2000; Brannon and Roitman 2003; Shettleworth 2010). For example, the representation of event number and duration may share a common accumulator mechanism (see review by Brannon and Roitman 2003). In our trials, forming larders consisting of more prey involved both a greater number of prey capture events (each of similar duration) and a longer total time, which could influence the representation of prey larders in memory. We speculate that spiders likely perceived each prey capture event separately, rather than all as a continuum. This is because there are many actions within each prey capture event (detecting and locating the prey on the web; extracting the prey from the sticky spiral of the web; bringing it to the hub to wrap it in silk and secure it; and feeding; see “Methods”). Thus, several prey capture events may leave a different memory from a single event. Nevertheless, it took longer to form larger larders, and further work will be required to address the event number/duration question. (And, if handling larger prey also takes longer, this too may contribute to an accumulator mechanism for representations of the size of single prey items.) What seems least likely is that *Nephila* representations of prey counts involved subitizing (whereby numerosities of 1–4 are perceived visually “at a glance”, rather than

counted) (Burr and Ross 2008; Brannon and Roitman 2003; Brannon and Cantlon 2009). This is because spiders did not perceive prey ladders visually but through web vibrations and touch and taste, and they did not perceive prey ladders as a single scene or tableau—except perhaps just prior to our removal of the ladders, although that also seems unlikely because each prey item was attached to the hub with a single silk line, and spiders fed on only one item at a time.

Searching for lost prey lasted for up to 15–20 min (and up to nearly 25 min in prior work; Rodríguez et al. 2013). These intervals offer an estimate for the time window during which memory of prey features remain active as an influence on the spiders' behavior. But these are minimum estimates, as we cannot distinguish between forgetting and adaptive giving up for searches (Rodríguez et al. 2013).

*Nephila* seemed to value ladders with greater prey counts more highly than equivalent prey quantities in the form of a single item, as they spent more effort in seeking to recover them. This view of the spiders' prey valuations counters the expectation that the foraging success of web spiders will benefit more from rare large prey rather than from common small prey (Venner and Casas 2005). But it is important to note that, for *Nephila*, selection on memory of prey features and its use in regulating searching efforts is likely to be related to the kleptoparasites that remove prey from their webs, which can inflict heavy costs (Robinson and Mirick 1971; Rysprtra 1981). In this context, it may be a safer investment to search when the lost ladder consisted of several prey items than when a single prey item was stolen; e.g., kleptoparasites may take longer to remove all items from the web rather than a single item, or several items may be more likely to be spread over a larger area of the web than a single item.

To find evidence suggestive of a sense of numerosity in *Nephila* spiders considerably expands the taxonomic and ecological diversity of numerosity in animals, with this report being the first for a spider other than jumping spiders (family Salticidae; Nelson and Jackson 2012). *Nephila* offer an intriguing combination of natural history features that variously influence what might be expected in terms of their cognitive and numerosity abilities. For sit-and-wait predators that rely on snaring prey with a web, there might seem to be little advantage for cognition to be involved in foraging ecology. Then again, a main feature of their ecology is the presence of kleptoparasites (Robinson and Mirick 1971; Rysprtra 1981) that might select for recovery efforts and using memory of the features of captured prey to regulate those efforts (Rodríguez et al. 2013). But other web spiders that lack kleptoparasites also form memories of prey features (Rodríguez and Gamboa 2000; Rodríguez and Gloudeman 2011). Broader comparative work will be necessary to understand how the particularities of *Nephila* natural history fit with the broader question of the evolution

of the sense of numerosity—and to understand the extent to which numerosity abilities represent a basic feature of animal brains or are shaped by selection stemming from the ecology of different species. Experiments conducted in the animals' own environments, using their natural behavior to provide the experimental assays, will bring novel insights into animal cognitive powers and how they relate to their ecology and the baseline abilities of their nervous systems.

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