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ORIGINAL PAPER

Estimating the repeatability of memories of captured prey formed by *Frontinella communis* spiders (Araneae: Linyphiidae)

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Abstract How animals deal with the challenges posed by their ecological and social surroundings often hinges on the acquisition and storage of information about those surroundings. That is, an animal's fitness may be influenced by variation in the mental representations it has formed of its environment. Studying such variation is challenging because it involves documenting inherently subjective phenomena. However, observations of behaviour may provide objective descriptions of mental representations. We used the behaviour of *Frontinella communis* spiders after removal of prey from their webs as an assay of the contents of their memories of the prey. Spiders searched for lost prey, exerting greater effort in searching for larger prey, and distinguishing between the object of the search and old prey remnants. We thus infer that spider memories included information about prey features such as size or quality. We found significant repeatability in the spiders' searching behaviour, suggesting repeatability in memory content. As an indication of consistent between-individual differences in searching and memory, these repeatability estimates suggest that selection may act to shape mental representations and their relationship with foraging behaviour.

Keywords Animal cognition · Cognitive ecology · Foraging · Web spider

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Introduction

Animals often use information about their surroundings to make decisions such as habitat choice and mate choice. Acquiring and processing such information—i.e. cognition—takes centre stage in an evolutionary dynamic between animals and their environments. In this dynamic, an animal's ecology and its mating and social systems influence the extent and form of its cognitive abilities (e.g. Balda and Kamil 1989; Madden 2001; Pravosudov and Clayton 2002; Day et al. 2005; Farris and Roberts 2005; Pitnick et al. 2006; Pollen et al. 2007; Gonda et al. 2009). In turn, cognitive abilities determine how animals relate to their environment, and they may even influence how selection shapes their behaviour (Real 1993; Healy and Braithwaite 2000; Dukas 2004; Sol et al. 2005; Overington et al. 2009). Understanding the evolution of behaviour thus requires assessing variation in the mental representations that animals form of their surroundings. This poses the challenge of gaining access to inherently subjective phenomena and doing so in a way that allows estimating genetic and selection parameters (Dukas 2004).

Variation in mental representations of the environment is often associated with behaviour that can be described objectively. For example, foraging theory hinges on information about resource quality and distribution. This need not involve cognition, since selection can confer a measure of 'information content' on behaviour, in the sense that selection favours behaviour that is adaptive in specific circumstances (Giraldeau 2008; Frank 2009; Hamilton 2010; Shettleworth 2010). Nevertheless, fine-tuning decisions frequently requires more flexibility than is allowed by fixed cue-response systems, and animals often make use of information that they have acquired personally or socially (Giraldeau et al. 2002; Coolen et al. 2005; Healy and Rowe

2010; Shettleworth 2010). In such cases, animal behaviour may reflect variation in the information stored in memory, and it may provide access to the content of animal memories.

An example of how descriptions of behaviour give access to mental representations of the environment occurs in web spiders whose behaviour reflects memory of the web's layout and contents (LeGuelte 1969; Suter 1978; Eberhard 1988; Rodríguez and Gamboa 2000; Opell 2001). We focus on spiders' searching behaviour, in which spiders walk around the web, tugging or plucking on its threads to obtain vibrational cues about its contents (Robinson and Olazarri 1971; Suter 1978; Barth 1982; Masters et al. 1986; Vollrath 2007). Searching often follows an immediate stimulus, such as prey being snared by the web or debris falling on it, and it can also represent brief reconnaissance following a disturbance (Robinson and Olazarri 1971; Foelix 1996; Rodríguez and Gamboa 2000). However, searching may also be prompted by memory of the layout and contents of the web. For example, experiments altering web orientation show that *Zygiella x-notata* (Araneidae) remember the location of their retreat and that when they do not find it, they search until they find it (LeGuelte 1969). Another araneid, *Cyclosa turbinata*, search when prey escape from their web before they have reached them (Suter 1978), and *Miagrammopes animotus* (Uloboridae) search for lost egg sacs (Opell 2001). Finally, in experiments with *Neriene peltata* (Linyphiidae), *Nephila clavipes* (Tetragnathidae) and *Argiope argentata* (Araneidae), spiders searched when recently captured prey were removed from their web; controls (involving various forms of sham prey removal) generally failed to elicit searching (Rodríguez and Gamboa 2000). We suggest that searching for lost prey indicates that spiders formed memories of the prey and that they expected to find it on the web. We further suggest that variation in searching behaviour may reflect the representation of prey features in memory.

Here, we use repeated trials with large and small prey to test hypotheses about the sources of variation in the searching behaviour of bowl and doily spiders, *Frontinella communis* (Araneae: Linyphiidae). Our goal was to assess the repeatability of searching for lost prey as a proxy for the repeatability of memory of captured prey, in order to assess the potential for the presence of variation in memory that selection may act upon. Repeatability is a measure of consistent between-individual differences, and it provides a baseline expectation for the presence of genetic variation (Lessells and Boag 1987; Lynch and Walsh 1998; Bell et al. 2009).

We first confirmed that *F. communis* form memories of captured prey that contain some details about the prey's features. We then estimated the repeatability of searching behaviour and tested hypotheses about whether these estimates reflect individual differences in memory or potentially confounding factors such as variation in boldness or motivation. (1) If *F. communis* form memories containing some details about the features of captured prey, they will search for stolen prey and search longer for larger prey. (2) We were able to test a corollary prediction of the memory hypothesis. Some webs contained remnants of prey the spiders had consumed previously. If searching reflects memory, spiders should continue searching after encountering the remnants. But if searching is prompted by proximate cues on the web or if the target of the search does not remain in memory due to confounding cues, spiders should stop searching when they encounter the remnants. (3) We estimated repeatability according to Lessells and Boag (1987). Our estimates of repeatability may reflect consistent individual differences in memory. However, they may also reflect differences in boldness (cf. behavioural syndromes; Sih et al. 2004; Bell 2007) or in motivation. We thus tested hypotheses designed to tease apart these sources of variation. (4) These tests are based on a practical requirement of our assay: removal of the prey from the web with minimum disturbance is possible for spider species that (upon light disturbance) retreat and leave the prey behind on the web, rather than take it in their mouthparts. We reasoned that differences in boldness or motivation would be most clearly at play when spiders are recovering from this light disturbance, before they start searching. Thus, the time to start searching is likely to reflect the influence of boldness or motivation, and we used it as a covariate in our analysis. This does not test for behavioural syndromes, since it involves only one behavioural context, but our goal was to account for variation in boldness or motivation. (5) Other potential confounding factors may involve variation in the motivation associated with familiarity with the experimental procedure (since it involved repeated trials). If so, there should be progressive changes in the spiders' behaviour along the sequence of trials.

Methods

We conducted the study during July–August 2009. We collected *F. communis* at UWM's Field Station (Saukville, WI), on a patch of juniper, *Juniperus communis*. We only used adult females. We kept voucher specimens (collections of RLR and of ML Draney, University of Wisconsin–Green Bay). In the laboratory, we kept spiders in individual plastic boxes (10 × 10 × 6.5 cm) lined with moist paper towels and covered with cling wrap. Prey were *Acheta domesticus* crickets (Fluker Farms, LA). To vary prey size and keep taste and smell constant, we used small and large cricket nymphs. Small prey were 1-week-old nymphs

(2nd–3rd instars; mean ± SE mass = 1.75 ± 0.04 mg; pronotum length = 0.46 ± 0.01 mm). Large prey were 3-week-old nymphs (5th–6th instars; mass = 8.78 ± 0.24 mg; pronotum length = 0.84 ± 0.01 mm). For comparison, the spiders' cephalothorax length was 1.36 ± 0.025 mm. We did not test controls (e.g. sham prey removal) to maximise sample size for our repeatability estimates. Instead, we base this study on prior work that tested such controls with spiders including another linyphiid (Rodríguez and Gamboa 2000).

As soon as spiders built a web (usually 1 day after collection), we fed them 1 small prey. Trials began the day after this feeding. Immediately after each trial, we fed spiders 1 small prey and waited 3 days before the next trial. Our purpose with these feedings was to minimise differences in hunger and motivation among spiders. At the time of capture, spiders likely varied in the size and recency of their last meal. Following capture, spiders had to invest in a new web before we could feed them. We therefore fed the spiders closer to their first trial than to the other trials. Our feedings amount to 3 × 1.75 mg/10 days = 0.52 mg/day or 0.3 prey/day. In the field, *F. communis* consume a median of 3.12 mg/day, or 3.3 prey/day, with median prey size = 1–1.9 mm (Suter 1985, 1990). Our feedings thus matched common field prey sizes, but at a fraction of prey numbers and mass. Consequently, our feedings likely did not satiate spiders. However, they kept the spiders far from any risk of starvation (Suter 1985). We consider that our feeding regime minimised differences in hunger and motivation whilst sustaining interest in prey capture.

A trial started when we lightly dropped prey on a spider's web. We allowed spiders to capture the prey and to begin to feed on it for 30 s. We then proceeded to remove the prey from the web. To minimise the disturbance of prey removal, we induced spiders to retreat from the prey by tapping on the web with a forceps or, if necessary, gently touching them on the cephalothorax with the forceps. We then carefully pulled the prey off the web with the forceps, either causing no damage to the web or leaving a small hole. These holes likely had a minimal effect, since linyphiids orientate on the web by gravity and tension patterns due to tensor lines at the bottom of the web (Suter 1984), which we did not damage.

After prey removal, we noted whether spiders searched or not, and we used a stopwatch to note the time to start searching and the time spent searching. (Observers were not blind to the treatments.) Spiders searched in bouts separated by intervals of quiescence. We report the time spent in search bouts (active search time) and in search bouts + intervening quiescent intervals (total search time).

Our criterion for whether searching occurred was conservative: we counted only searches >30 s, to avoid including reconnaissance plucks. This excluded 3 trials, each with a different spider. Our criterion for when searches ended was based on preliminary observations ($n = 15$), wherein spiders that had searched and then been quiescent for 20 min continued not to move for an additional 40 min of observation. We therefore considered that searches ended when spiders remained quiescent for 20 min.

We aimed to test each individual spider 4 times, twice with each prey size, in random order. Of 69 spiders that we collected, 41 built webs and entered the trials and 33 completed all trials. We lost 8 spiders because they walked out of their web, incurred web damage during prey removal or retreated with the prey in their mouthparts.

The webs of 12 spiders contained remnants of old prey they had consumed previously, and we noted how the spiders reacted when they came across them during searching in our trials.

Statistical analysis

We assessed repeatability with the term for spider individual identity (spider ID), following Lessells and Boag (1987).

Likelihood of searching

We used a mixed-model binomial logistic regression to test whether the likelihood of searching was influenced by spider ID (random effect) and by prey size and trial sequence (fixed effects). We conducted this analysis in R (http://www.R-project.org) with the glmer function of the *lme4* package (code available upon request). This analysis provides variance component estimates for random effects and significance tests for fixed effects. We then obtained significance for the spider ID term by comparing the full model with a model that excluded this term.

Searching time

With $n = 33$ spiders, we had relatively few degrees of freedom. We thus ran the analysis in two steps. (1) We used a linear mixed model in JMP 7.0.1 (SAS Institute, NC) to test whether the spiders' behaviour was influenced by spider ID (random effect) and by prey size and trial sequence (fixed effects). We refer to this model as model 1. It corresponds to the 'random regression' method of implementing a repeated measures design in JMP. Our purpose in this step was to obtain a significance test for spider ID. We estimated repeatability from the variance component of this term, after confirming that it corresponds exactly to the procedure in Lessells and Boag (1987). We also estimated repeatability for behaviour with large and small prey separately, from a model including only spider

ID (random effect) and trial sequence (fixed effect). (2) We used a linear mixed model implemented with Restricted Maximum Likelihood (REML) in JMP that included the following terms: spider ID (random effect), prey size and trial sequence (fixed effects), spider ID × prey size interaction (random effect), spider ID × trial sequence (random effect). When the dependent variable was active or total search time, we also included the time to start searching as a covariate. We refer to this model as model 2. With it, we aimed to increase the statistical power of the tests of the fixed effects (prey size, trial sequence) and to account for the potential influence of boldness or motivation on searching behaviour. Nevertheless, with $n = 33$, we had low statistical power to detect differences in behaviour across prey sizes. We thus complemented our analysis with an effect-size approach (Cohen 1988; Nakagawa and Cuthill 2007). We described differences in searching for large and small prey with Cohen's d (Cohen 1988; Borenstein et al. 2009):

$$\text{Cohen's } d = |\text{mean}_1 - \text{mean}_2|/\text{pooled SD}$$

$$\text{where pooled SD} = \sqrt{[((n_1 - 1)\text{SD}_1^2 + (n_2 - 1)\text{SD}_2^2)/(n_1 + n_2 - 2)]}$$

We then converted d to a coefficient, r, that is bounded between 0 and 1 and that allows expressing effect sizes in standard categories of small ($r < 0.30$), medium ($0.30 \leq r < 0.50$) or large ($r \geq 0.50$) magnitude. The conversion from d to r when sample sizes are equal is:

$$r = d/\sqrt{(d^2 + 4)}$$

Because sample sizes for large and small prey were equal or differed by only 1 individual, these estimates of effect size are unbiased.

Results

Spiders searched for lost prey and searched longer for larger prey

Of 33 spiders that completed all trials, 97% searched in at least one trial and 61% searched in all trials. The likelihood of searching varied consistently between individuals (spider ID term: $\chi_1^2 = 5.34$, $P = 0.021$) but was not significantly influenced by prey size or trial sequence ($P \geq 0.18$). On average, 83 ± 0.1% of spiders searched for small prey and 80 ± 0.1% searched for large prey. Spiders thus showed consistent individual variation in the likelihood of searching for lost prey, but they did not appear to modulate the likelihood of searching according to prey size.

Spiders started searching sooner for larger prey. However, this difference was non-significant (Table 1) and of small effect size ($d = 0.29$, $r = 0.14$; Fig. 1a, black line).

Spiders searched longer for larger prey (Fig. 1b, black line). This effect was not significant, but we consider that this was due to low statistical power (note the magnitude of the F-ratio; Table 1). With $n = 33$ spiders, statistical power was adequate ($1-\beta \geq 0.80$) only for a difference ≥2.6 min (vs. our detected difference of 2.21 min). We thus used an effect size criterion to evaluate the importance of the difference in active search times for large versus small prey. The effect size of this difference was near the high end of the small effect size category: 2.21 min corresponds to 28% longer searches for large prey, or an effect size of $d = 0.43$, $r = 0.21$ (Fig. 1b). Spiders also showed longer total search times (time in search bouts + intervening quiescent intervals) for larger prey (Fig. 1c, black line). However, this difference was non-significant and of small effect size (2.20 min, corresponding to 18% longer searches for large prey; $d = 0.26$, $r = 0.13$).

Because the differences in active and total search times were so similar (2.21 and 2.20 min, respectively), we consider that total search time reflects the difference in active search time for large versus small prey, plus similar amounts of quiescence between bouts of searching. We thus interpret active search time as indicative of the content of memories of captured prey and total search time as indicative of the time over which spiders retained those memories (and a minimum indication at that, since spiders may have given up rather than forgotten). Maximum total search times for large and small prey were 39.4 and 42.4 min, respectively.

Spiders continued searching even when they encountered old prey remnants

All 12 spiders whose webs contained remnants of old prey inspected the remnants briefly (1–5 s) during searching, usually within the first 30 s. All spiders then resumed searching, and they sometimes briefly re-examined the remnants (3–5 times, ca. 1 s each). Because these inspections were so brief, we consider that they did not have a confounding effect on our measures of search times.

Repeatability

Spiders varied consistently in the likelihood of searching, as well as in the time to begin searching and in active and total search times (Table 1). Repeatability had low to medium magnitude when calculated across prey sizes (Table 1). For large prey only, repeatability had high magnitude, but for small prey only, it was of low magnitude and non-significant (Table 1). This difference in repeatability for behaviour with large and small prey likely reflects lower between-individual variation when searching for small prey (Fig. 1a–c, grey lines).

Table 1 Sources of variation in the behaviour of *F. communis* after removal of prey from their web

Behaviour	Source of variation	*F* test	Repeatability		
			Across prey sizes	Large prey	Small prey
Time to begin search	Spider ID	**$F_{27,\ 60} = 2.05$, $P = 0.011$**	**$r = 0.25$**	**$r = 0.42$, $P = 0.05$**	$r = 0.16$, $P = 0.27$
	Prey size	$F_{1,\ 23.16} = 1.53$, $P = 0.23$			
	Trial sequence	**$F_{1,\ 24.55} = 8.77$, $P = 0.0067$**			
Active search time	Spider ID	**$F_{31,\ 72} = 1.67$, $P = 0.038$**	**$r = 0.17$**	**$r = 0.60$, $P = 0.0013$**	$r = -0.17$, $P = 0.78$
	Prey size	$F_{1,\ 12} = 3.92$, $P = 0.071$			
	Trial sequence	$F_{1,\ 18.32} = 0.01$, $P = 0.95$			
	Time to begin search	**$F_{1,\ 39.21} = 13.2$, $P = 0.0008$**			
Total search time	Spider ID	**$F_{31,\ 72} = 1.68$, $P = 0.0385$**	**$r = 0.17$**	**$r = 0.52$, $P = 0.0078$**	$r = -0.07$, $P = 0.65$
	Prey size	$F_{1,\ 24.6} = 1.13$, $P = 0.30$			
	Trial sequence	$F_{1,\ 26.64} = 0.95$, $P = 0.34$			
	Time to begin search	**$F_{1,\ 80.06} = 6.51$, $P = 0.013$**			

Significance for spider ID (random effect) from model 1 (see 'Statistical analysis') provides the significance of repeatability across prey sizes. Significance for prey size and trial sequence obtained from model 2 (see 'Statistical analysis'). Significance indicated in boldface. Not shown: spider ID × prey size and spider ID × trial sequence interactions, as the REML method in model 2 does not provide significance for random effects

Memory versus boldness, motivation and hunger

We expected any effects of variation in boldness to be most clearly manifest during recovery from the disturbance of prey removal (i.e. in the time to start searching). Indeed, spiders that started to search sooner also searched longer (Table 1; Fig. 2). This suggests that boldness or motivation (as well as memory) may have influenced the time to start searching and search times. We therefore included the time to start searching as a covariate in model 2 (see 'Statistical analysis') to remove these potential contributions of boldness or motivation from the test of the effect of prey size (Table 1; Figs. 1, 2).

We expected variation due to experiment-wide changes in motivation, hunger or familiarity with the experiment to be manifest as progressive changes in the spiders' behaviour along the sequence of trials. Trial sequence had a significant and progressive effect on the time to start searching, but not on search times (Table 1; Fig. 1d–f).

Discussion

Frontinella communis spiders searched for lost prey. They were equally likely to search for large and small prey, but they searched longer for large prey. Spiders also distinguished between searched-for prey and old prey remnants, indicating that the target of their search remained in their memory in spite of confounding cues. Overall, spiders spent substantial effort searching for lost prey, up to ca. 40 min of total search time. We found significant repeatability in the likelihood of searching and in searching behaviour. We attempted to minimise differences in hunger and motivation across spiders, but variation in boldness and motivation likely influenced the spiders' behaviour. We attempted to remove these confounding factors from the test of the effect of prey size on searching behaviour (using the time to start searching as a covariate), and we consider that active search times provide a good indication of memory content.

We conclude that *F. communis* formed memories of captured prey that included details about prey features such as size and that those memories varied consistently across individuals. Repeatability of search times varied according to whether it was calculated across prey sizes or separately for large and small prey. Across prey sizes, repeatability was on the medium range of the small effect size category ($r = 0.17$; Table 1). This is low compared with estimates for the repeatability of foraging or exploratory behaviour or of the behaviour of arachnids ($r \approx 0.5$; Bell et al. 2009).

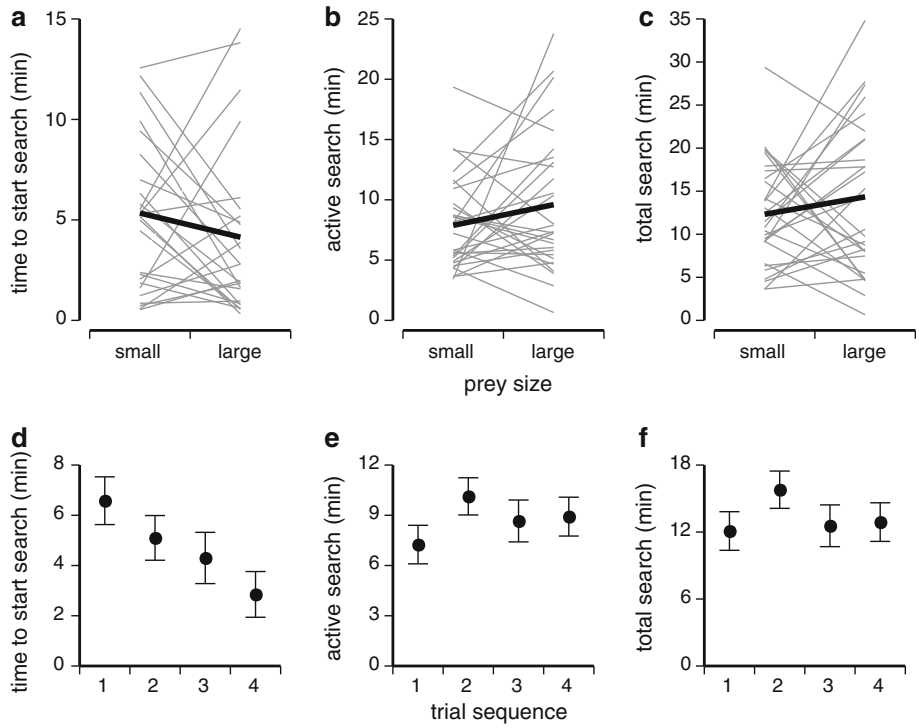

Fig. 1 Behaviour of *F. communis* following removal of prey from their web. **a**, **b**, **c** Effect of prey size on the time to start searching and on active and total search times. *Thick black lines* show least square means ± 1SE obtained from model 2 (see 'Statistical analysis'). *Thin grey lines* show mean times for individual spiders. **d**, **e**, **f** Effect of the trial sequence on the time to begin searching and on active and total search times. We show least square means ± 1SE obtained from model 2 (see 'Statistical analysis')

However, repeatability of search times encompasses not only a specific behaviour (searching) but also—according to our interpretation—memory of captured prey. The greater complexity of the cognitive and behavioural processes underlying this estimate may account in part for its small magnitude. On the other hand, repeatability of search times for large prey was high ($r = 0.60$), whereas for small prey it was very small (Table 1). That is, individual differences were more consistent for large prey than across prey sizes and more consistent across prey sizes than for small prey. Thus, selection may be more efficient in changing memory and behaviour related to large prey or in changing the sign and steepness of the difference between memory and behaviour with large and small prey (grey lines in Fig. 1a–c). Conversely, selection may be less efficient in changing aspects related to responses to small prey.

Significant repeatability in searching behaviour is consistent with the hypothesis that some of the variation—and some associated variation in memory content—may represent genetic variation (Lessells and Boag 1987; Lynch and Walsh 1998; Bell et al. 2009). We note that repeatability may underestimate or overestimate genetic variation, and demonstrating genetic variation requires quantitative genetics experiments. We are thus cautious in interpreting our findings as suggesting genetic variation. However, we also note that environmental causes of variation capable of creating consistent between-individual differences are also relevant for the response to selection and evolutionary divergence (e.g. West–Eberhard 2003, 2005).

Our findings tentatively suggest that memory of captured prey and associated behaviour may have the capacity to be shaped by selection. How web spiders deal with the risk of prey loss may include using such memories to regulate prey recovery efforts. For example, some spiders are afflicted by kleptoparasites that remove prey from the web or consume it on the web (Robinson and Olazarri 1971; Vollrath 1979; Foelix 1996; Grostal and Walter 1997), and searching may help them recover prey. Even without kleptoparasites, searching may help find prey that are moved by wind, or in cases in which spiders wrap up prey and return to the hub leaving the prey at the site of capture. Memory may also help regulate searching effort according to prey value, and it may also prevent prematurely ending a search when encountering old prey remnants. Spiders may differ in the risk of prey loss (e.g. prey escape rates in the interval between interception by the web and the spider arriving at the site range from 10 to 80% among orb-weaver species; Eberhard 1990). Selection on memory may thus vary between species and promote divergence in the acquisition and use of information about captured prey.

Selection on memory and associated behaviour may also arise from the broader relationship between web-building and cognition in spiders. For example, web spiders use

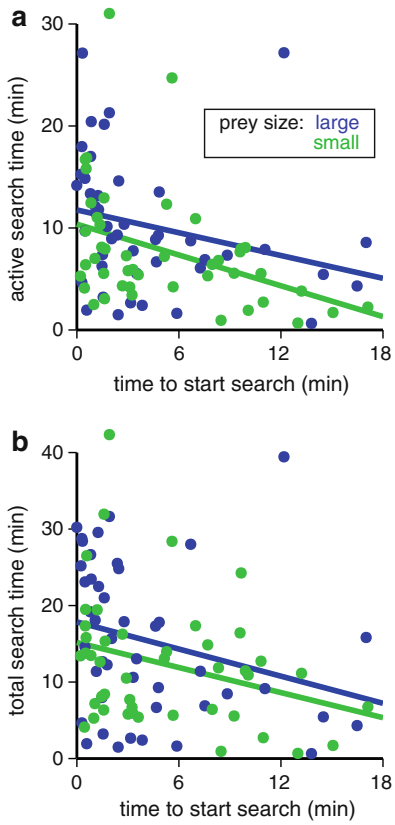

Fig. 2 Negative relationship between the time to start searching and active (**a**) and total (**b**) search times for *F. communis* that captured and lost large and small prey. Spiders that started to search sooner also searched longer. Nevertheless, across times to start searching, spiders searched longer for large prey than for small prey (*blue* vs. *green lines*, respectively)

information about their ecological and social environments to make decisions about preferred prey and about web construction, architecture and relocation (Turnbull 1960; Riechert and Gillespie 1986; Sandoval 1994; Heiling and Herberstein 1999; Herberstein et al. 2000; Venner et al. 2000; Watanabe 2000; Nakata et al. 2003; Nakata 2007, 2008, 2009; Salomon 2009; Rittschof and Ruggles 2010). Spider diversification has involved changes in web architecture and web-building behaviour (including web loss; Shear 1986; Vollrath and Selden 2007; Blackledge et al. 2009). Different web types have different costs to build and replace (Eberhard 1986; Blackledge et al. 2009), and spiders with costlier webs may be more strongly selected to prevent prey loss. On the other hand, increases in behavioural complexity associated with derived webs (Blackledge et al. 2009) may facilitate increases in cognition. In short, cognition and behaviour related to memory of the content of webs may be involved in the evolutionary interplay between web architecture and spider ecology.

The sample of spiders that have been tested for memory of captured prey (Rodríguez and Gamboa 2000; this paper) includes orb-weavers (Araneidae, Tetragnathidae) and spiders derived from them (Linyphiidae). Although these tests suggest that memory of captured prey may be widespread within this group, all of these species have highly derived webs and behaviour, and it will be interesting to study spiders with other derived web types (e.g. Theridiids) or with more basal webs such as sheet webs (Vollrath 2007; Blackledge et al. 2009).

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References

Balda RP, Kamil AC (1989) A comparative study of cache recovery by three corvid species. Anim Behav 38:486–495

Barth FG (1982) Spiders and vibratory signals: sensory perception and behavioral significance. In: Witt PN, Rovner JS (eds) Spider communication. Mechanisms and ecological significance. Princeton University Press, NJ, pp 68–122

Bell AM (2007) Future directions in behavioural syndromes research. Proc R Soc B 274:755–761

Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. Anim Behav 77:771–783

Blackledge TA, Scharff N, Coddington JA, Szüts T, Wenzel JW, Hayashi CY, Agnarsson I (2009) Reconstructing web evolution and spider diversification in the molecular era. Proc Natl Acad Sci USA 106:5229–5234

Borenstein M, Hedges LV, Higgins JPT, Rothstein HR (2009) Introduction to meta–analysis. Wiley, Sussex

Cohen J (1988) Statistical power analysis for the behavioral sciences, 2nd edn. Lawrence Erlbaum Associates, NJ

Coolen I, Dangles O, Casas J (2005) Social learning in noncolonial insects? Curr Biol 15:1931–1935

Day LB, Westcott DA, Olster DH (2005) Evolution of bower complexity and cerebellum size in bowerbirds. Brain Behav Evol 66:62–72

Dukas R (2004) Evolutionary biology of animal cognition. Annu Rev Ecol Evol Syst 35:347–374

Eberhard WG (1986) Effects of orb-web geometry on prey interception and retention. In: Shear WA (ed) Webs behavior and evolution. Stanford University Press, CA, pp 70–100

Eberhard WG (1988) Memory of distances and directions moved as cues during temporary spiral construction in the spider *Leucauge mariana* (Araneae: Araneidae). J Insect Behav 1:51–66

Eberhard WG (1990) Function and phylogeny of spider webs. Annu Rev Ecol Syst 21:341–372

Farris SM, Roberts NS (2005) Coevolution of generalist feeding ecologies and gyrencephalic mushroom bodies in insects. Proc Natl Acad Sci USA 102:17394–17399

Foelix RF (1996) Biology of spiders, 2nd edn. Oxford University Press, NY

Frank SA (2009) Natural selection maximizes Fisher information. J Evol Biol 22:231–244

Giraldeau LA (2008) Solitary foraging strategies. In: Danchin E, Giraldeau LA, Cézilly F (eds) Behavioural ecology. Oxford University Press, NY, pp 233–255

Giraldeau LA, Valone TJ, Templeton JJ (2002) Potential disadvantages of using socially acquired information. Phil Trans R Soc Lond B 357:1559–1566

Gonda A, Herczeg G, Merilä J (2009) Adaptive brain size divergence in nine-spined sticklebacks (*Pungitius pungitius*)? J Evol Biol 22:1721–1726

Grostal P, Walter DE (1997) Kleptoparasites or commensals? Effects of *Argyrodes antipodianus* (Araneane: Theridiidae) on *Nephila plumipes* (Aranenae: Tetragnathidae). Oecologia 111:570–574

Hamilton IM (2010) Foraging theory. In: Westneat DF, Fox CW (eds) Evolutionary behavioral ecology. Oxford University Press, NY, pp 177–193

Healy S, Braithwaite V (2000) Cognitive ecology: a field of substance? Trends Ecol Evol 15:22–26

Healy SD, Rowe C (2010) Information processing: the ecology and evolution of cognitive abilities. In: Westneat DF, Fox CW (eds) Evolutionary behavioral ecology. Oxford University Press, NY, pp 162–174

Heiling AM, Herberstein ME (1999) The role of experience in web–building spiders (Araneae). Anim Cognit 2:171–177

Herberstein ME, Gaskett AC, Glencross D, Hart S, Jaensch S, Elgar MA (2000) Does the presence of potential prey affect web design in *Argiope keyserlingi* (Araneae, Araneidae)? J Arachnol 28:346–350

LeGuelte L (1969) Learning in spiders. Am Zool 9:145–152

Lessells CM, Boag PT (1987) Unrepeatable repeatabilities: a common mistake. Auk 104:116–121

Lynch M, Walsh B (1998) Genetics and analysis of quantitatie traits. Sinauer Associates, MA

Madden J (2001) Sex, bowers and brains. Proc R Soc Lond B 268:833–838

Masters WM, Markl HS, Moffat AJM (1986) Transmission of vibration in a spider's web. In: Shear WA (ed) Webs behavior and evolution. Stanford University Press, CA, pp 49–69

Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol Rev 82:591–605

Nakata K (2007) Prey detection without successful capture affects spider's orb–web building behaviour. Naturwissenschaften 94:853–857

Nakata K (2008) Spiders use airborne cues to respond to flying insect predators by building orb–web with fewer silk thread and larger silk decorations. Ethology 114:686–692

Nakata K (2009) To be or not to be conspicuous: the effects of prey availability and predator risk on spider's web decoration building. Anim Behav 78:1255–1260

Nakata K, Ushimaru A, Watanabe T (2003) Using past experience in web relocation decisions enhances the foraging efficiency of the spider *Cyclosa argenteoalba*. J Insect Behav 16:371–380

Opell BD (2001) Egg sac recognition by female *Miagrammopes animotus* (Araenae, Uloboridae). J Arachnol 29:244–248

Overington SE, Morand–Ferron J, Boogert NJ, Lefebvre L (2009) Technical innovations drive the relationship between innovativeness and residual brain size in birds. Anim Behav 78:1001–1010

Pitnick S, Jones KE, Wilkinson GS (2006) Mating system and brain size in bats. Proc R Soc B 273:719–724

Pollen AA, Dobberfuhl AP, Scace J, Igulu MM, Renn SCP, Shumway CA, Hofmann HA (2007) Environmental complexity and social organization sculpt the brain in Lake Tanganyikan cichlid fish. Brain Behav Evol 70:21–39

Pravosudov VV, Clayton NS (2002) A test of the adaptive specialization hypothesis: population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). Behav Neurosci 116:515–522

Real LA (1993) Toward a cognitive ecology. Trends Ecol Evol 8:413–417

Riechert SE, Gillespie RG (1986) Habitat choice and utilization in web–building spiders. In: Shear WA (ed) Webs behavior and evolution. Stanford University Press, CA, pp 23–48

Rittschof CC, Ruggles KV (2010) The complexity of site quality: multiple factors affect web tenure in an orb–web spider. Anim Behav 79:1147–1155

Robinson MH, Olazarri J (1971) Units of behavior and complex sequences in the predatory behavior of *Argiope argentata* (Fabricius): (Araneae: Araneidae). Smithson Contrib Zool 65:1–36

Rodríguez RL, Gamboa E (2000) Memory of captured prey in three web spiders (Araneae: Araneidae, Linyphiidae, Tetragnathidae). Anim Cognit 3:91–97

Salomon M (2009) Social environment and feeding state influence movement decisions in a web–building spider. Ethology 115:916–927

Sandoval CP (1994) Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. Funct Ecol 8:701–707

Shear WA (1986) The evolution of web–building behavior in spiders: a third generation hypothesis. In: Shear WA (ed) Webs behavior and evolution. Stanford University Press, CA, pp 364–400

Shettleworth SJ (2010) Cognition, evolution, and behavior, 2nd edn. Oxford University Press, NY

Sih A, Bell AM, Johnson JC, Ziemba RE (2004) Behavioral syndromes: an integrative overview. Q Rev Biol 79:241–277

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L (2005) Big brains, enhanced cognition, and response of birds to novel environments. Proc Natl Acad Sci USA 102:5460–5465

Suter RB (1978) *Cyclosa turbinata* (Areneae: Araneidae): prey discrimination via web–borne vibrations. Behav Ecol Sociobiol 3:283–296

Suter RB (1984) Web tension and gravity as cues in spider orientation. Behav Ecol Sociobiol 16:31–36

Suter RB (1985) Intersexual competition for food in the bowl and doily spider, *Frontinella pyramitela* (Araneae, Linyphiidae). J Arachnol 13:61–70

Suter RB (1990) Determinants of fecundity in *Frontinella pyramitela* (Araneae, Linyphiidae). J Arachnol 18:263–269

Turnbull AL (1960) The prey of the spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). Can J Zool 38:859–873

Venner S, Pasquet A, Leborgne R (2000) Web-building behaviour in the orb–weaving spider *Zygiella x–notata*: influence of experience. Anim Behav 59:603–611

Vollrath F (1979) Vibrations: their signal function for a spider kleptoparasite. Science 205:1149–1151

Vollrath F (2007) The role of behavior in the evolution of spiders, silks, and webs. Annu Rev Ecol Evol Syst 38:819–846

Vollrath F, Selden P (2007) The role of behavior in the evolution of spiders, silks, and webs. Annu Rev Ecol Evol Syst 38:819–846

Watanabe T (2000) Web tuning of an orb–web spider, *Octonoba sybotides*, regulates prey-catching behaviour. Proc R Soc Lond B 267:565–569

West–Eberhard MJ (2003) Developmental plasticity and evolution. Oxford Univ, Press, NY

West–Eberhard MJ (2005) Developmental plasticity and the origin of species differences. Proc Natl Acad Sci USA 102:6543–6549