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Comments/Reflections

Insightful behaviour in arthropods?

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Abstract
Arthropod behaviour is usually explained through 'hard-wired' motor routines and learning abilities that have been favoured by natural selection. We describe observations in which two arthropods solved rare and perhaps completely novel problems, and consider four possible explanations for their behaviours: (i) the behaviour was a pre-programmed motor routine evolved to solve this particular problem, or evolved for other functions but pre-programmed to be recruited for this function under certain conditions; (ii) it was learned previously; (iii) it resulted by chance; or (iv) it was the result of insightful behaviour. Pre-programmed solutions can be favoured by natural selection if they provide solutions to common or crucial problems. Given the apparent rarity of the problems that these animals solved, the solutions they employed are unlikely to represent innate behaviour. Learning and random chance seem unlikely, although we cannot rule them out completely. Possibly these animals employed some degree of insight.

Keywords
insight, problem-solving, intelligent behaviour, motor routines, innovative flexibility.

1. Introduction

The cognitive abilities involved in problem solving vary widely among animals (Shettleworth, 2010). A key question is 'insight': can some animals

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'think' about a problem, 'understand' it, and then solve it (Shettleworth, 2012)? Can animals interrogate and manipulate a mental representation of their surroundings to work out a novel solution that they anticipate will work (Byrne, 2016)?

One of the main ways of testing for insight is to confront animals with an 'evolutionarily novel' problem, and assess whether they solve it in a way that is both innovative and expressed without practice. One commonly used method is the 'string-pulling test', in which the animal must 'realize', without trial-and-error learning, that the way to obtain a desired item is to pull on a string repeatedly while holding already-gathered portions of the string (e.g., Heinrich & Bugnyar, 2005; Alem et al., 2016). The requirement of novelty in the problem and in the solution follows the tradition in studies of animal behaviour to apply Morgan's Canon, that an action should not be interpreted as the outcome of the exercise of a higher cognitive faculty if it can be interpreted as the outcome of the exercise of a faculty lower in the psychological scale (Morgan, 1894). This criterion is probably too stringent and not necessarily parsimonious (Fitzpatrick, 2008), but we accept it here as useful (Zentall, 2018) in comparing the insight hypothesis with alternative explanations (see below).

One difficulty with standardized methods like the string-pulling test is that they restrict the diversity of species that can be tested (e.g., to animals able to sense a desired item at a distance, and to pull on and hold accumulated string) (Jacobs & Osvath, 2015). Such techniques seem particularly inappropriate for testing arthropods, a giant, hugely diverse group of animals in which some species show indications of insightful behaviour (Jackson & Cross, 2011; Loukola et al., 2017; Perry et al., 2017; Cross et al., 2020). Observations of behaviour under natural conditions can help pinpoint unusual problems for which pre-programmed, hard-wired or learned solutions are unlikely to exist. However, these natural but rare circumstances may be difficult to recreate experimentally. The two sets of observations that we report here in response to this special call for anecdotes in animal behaviour serve to expand the range of observations of possibly insightful behaviour to an increased diversity of animals. We describe evidence supporting two key features of problem-solving by insight: (i) impasse — where neither the animal's pre-programmed nor learned behaviour is sufficient to solve a problem; followed by (ii) an apparently evolutionarily novel solution arrived at without trial and error (Shettleworth, 2012). We discuss whether the behaviour of the animals we observed is likely to be explained by either pre-programmed solutions, including the possibility that these animals used pre-existing programs to recruit pre-programmed motor routines of particular appendages to other appendages when the original appendages were not available (e.g., due to leg loss; see Wilson, 1966), or by learning. We also consider two additional hypotheses: that their behaviour represented random variations, or that they modified and transfered pre-existing routines between appendages in an insightful way. We do not present these arguments as general tests of the hypotheses, but only to draw limited implications regarding these particular observations.

The anecdotes were recorded by different observers, and involve different species. We therefore present them separately, beginning each account with background information and ending with a discussion of the possibility that insight played a part in the animal's solution. They share the common feature of demonstrating that 'smaller-brained' animals can solve uncommon, perhaps completely novel problems, thus contributing to more general discussions that relate brain size to behavioural capabilities (Logan et al., 2018).

2. A new use for chelicerae in the golden-orb weaver *Trichonephila clavipes* (Araneae: Nephilidae) (RLR and GH)

The following field observation was conducted with a mature female golden-orb spider on January 2014, at San Pedro, San José, Costa Rica (at the end of the season of abundance at this highly seasonal site). When we encountered this spider, she was missing 5 of her 8 legs but on an orb (we did not observe the web in detail). This species naturally automatizes legs, but loss of 5 legs (or at least survival after such a loss) is exceedingly rare in the field (Table 1). Not a single case among the sample of 2513 observations in various surveys lacked more than three legs (Table 1). We know, however, of another three-legged mature female that constructed functional webs that had irregular sticky spiral spacing during several weeks, and that was repeatedly seen feeding (at least sometimes on prey that would normally require wrapping). She had a large abdomen and thus appeared to be well-fed (G. Barrantes, pers. comm.).

Table 1.
Abundance of *Trichonephila clavipes* individuals missing one to three legs in the field.

% spiders lacking $\geqslant$ 1 leg	Stage	Site	Date	Reference
2.8% of 290	Adult and subadult	San Antonio de Escazú, Costa Rica	16–20 August 2020	W.G. Eberhard, unpubl.
10.9% of 293	Adult and subadult	San Antonio de Escazú, Costa Rica	16 September 2020	W.G. Eberhard, unpubl.
9% of 162	Adult and subadult	San Antonio de Escazú, Costa Rica	8 November 2020	W.G. Eberhard, unpubl.
13% of 97	Adult and subadult	San Antonio de Escazú, Costa Rica	15 December 2020	W.G. Eberhard, unpubl.
31% of 59	Adult and subadult	La Selva, Costa Rica	February 2014	I. Escalante, unpubl.
3% of 263	Adult	University of Houston, Coastal Center, Texas, USA	August–September 1984, May 1988	Higgins (1992)
22% of 285	Adult	Los Tuxtlas, Mexico	August–October 1986, May 1987	Higgins (1992)
34% of 1064	Adult	Barro Colorado Island, Panama	January 1985–August 1986	Higgins (1992)

The following observation concerns the first of the above-mentioned three-legged spiders. We placed an insect on her web (a frozen, then thawed mealworm approx. 20–30% of the length of the spider's body). It was too large for her to use the *T. clavipes* prey-capture sequence for small prey such as midges, which is simply to extract it from the web and consume it while holding it in her chelicerae, without wrapping. She removed the prey from the web by grasping it in her chelicerae, and carried it to the hub of the web in her chelicerae. These actions are all part of the extensively-studied prey capture behaviour of *T. clavipes* (Robinson et al., 1969; Robinson & Mirick, 1971) and the closely related species *Nephila pilipes* (= *maculata*) (Hingston, 1922; Robinson & Robinson, 1973). However, she then failed in apparent attempts to complete the usual movements involved in the capture of large prey, in which the spider uses her anterior legs (I and II) to hold on to the web, other legs (III) and the palps to hold and rotate the prey, and yet other legs (IV) to wrap the prey by applying lines pulled from her spinnerets to the prey (Figure 1a) (Hingston, 1922; Figure 21 of Robinson & Robinson, 1973), prior to attaching the prey to the hub. Eventually the prey dropped to the ground.

We repeated the trial the next day with another mealworm. This time, when the spider reached the point in the sequence where she had failed the day before, she employed an unexpected solution to her quandary: she grasped the web with her cheliceral fangs to sustain her weight while she wrapped the prey. She then attached the prey to the web and fed on it.

Using the chelicerae to grasp the web in order to sustain the spider's weight is a novel behaviour. We know of only two remotely similar types of behaviour by intact *T. clavipes*. Spiders often grasp single lines or masses of lines with their cheliceral fangs to cut them (using an enzyme at the mouth) (Eberhard, in press). But the chelicerae exercise little force on these lines; instead the legs and palps pull the lines to the mouth region. Spiders pull strongly using their chelicerae when they are removing a large prey from the web after envenomating it (Figure 1b); but in this case the chelicerae hold the prey itself, not web lines, and the spider's weight is sustained by its legs rather than by the chelicerae. To our knowledge grasping silk lines with the chelicerae to support the spider's weight has never been described in this species (or any other spider); it is not mentioned in the extensive behavioural studies of this species and its close relatives by Robinson and colleagues (Robinson et al., 1969; Robinson & Mirick, 1971; Robinson & Robinson,

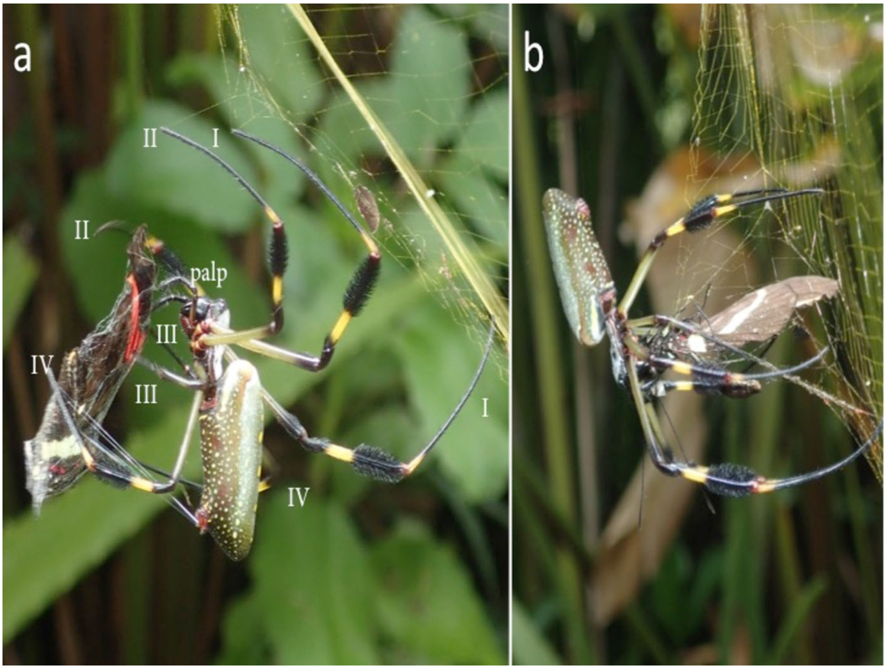

Figure 1. (a) A mature female *Trichonephila clavipes* wrapping a prey item sustains her weight with legs I and II, holds and turns the prey with legs III and the palps, and pulls wrapping silk from her spinnerets and lays it onto the prey with legs IV. (b) The same spider pulls a prey from her web, pushing on the web with her legs while pulling on it with her chelicerae.

1973), and we have never seen it before in several collective decades of watching orb-weaving spiders (RLR, GH & WGE, unpubl.; G. Barrantes, pers. comm.).

We suggest that this spider arrived at an insightful innovation, and that this consisted of using a pre-existing behaviour pattern (grasp lines with the chelicerae) in a new context to solve an evolutionarily novel problem. We are confident that the spider did not have a pre-programmed behavioural program of ‘sustain-weight-by-grasping-lines-with-the-chelicerae-when-legs-are-unavailable-for-this-task’, because selection for such behaviour is extremely unlikely. Loss of five legs is clearly very rare. For this same reason, we do not believe that a pre-existing program that prompts transfer of motor routines between legs and chelicerae exists. We do not know what previous experiences this spider had, and are thus not certain whether learning occurred. However, her failure to wrap the first mealworm suggests she was not familiar with this problem.

3. Unconventional defensive behaviour of *Stenolemus giraffa* (Hemiptera: Reduviidae) (FGS)

Stenolemus giraffa assassin bugs feed almost exclusively on web-building spiders of several families (Soley et al., 2011). *Stenolemus giraffa* rely on stealth to approach spiders, and attack them at their resting sites using their raptorial front legs. The bugs minimize web vibrations that they produce as they walk through the spiderweb and when breaking threads that block their path (Soley & Taylor, 2012, 2013; Soley, 2016). Nevertheless, *S. giraffa* are often detected and attacked by the resident spiders, and occasionally, *S. giraffa* is killed and consumed by its intended prey (Soley et al., 2011; Soley & Taylor, 2012, 2013). In most of these instances (96% of 415 approaches by spiders), the bugs reacted by remaining still, walking away, or crouching, flexing their mid and hindlegs to pull their body away from the spiders (Soley & Taylor, 2013). In most cases, the spider ceased its attack at this point and returned to its resting site (Soley & Taylor, 2013). Rarely (4% of 415 approaches by spiders), *S. giraffa* responded by striking at the spider with its forelegs (Soley & Taylor, 2013). Striking is a sudden extension and flexion of the forelegs, and represents characteristic predatory behaviour in this subfamily of bugs (Soley et al., 2011) and other insects with raptorial forelegs (Weirauch et al., 2011). Although predatory strikes at undisturbed spiders were often successful (59% of 32), strikes directed at approaching spiders rarely succeeded in capturing them (12% of 17 strikes, Soley & Taylor, 2013), but they often caused the spider to retreat (83% of 15 strikes) and may thus also have a defensive function (Soley & Taylor, 2013). Occasionally, a *S. giraffa* that was trapped in silk or grasped by a spider reacted by 'bucking' (forceful up-and-down movements produced by repetitive flexion-extension of middle and hind legs) or stridulating (rubbing its rostrum against its thorax) (Soley & Taylor, 2013).

On November 18, 2008, an interaction was staged between an adult female *S. giraffa* and *Pholcus phalangioides*, a non-native spider in the same family as *Trichocyclus* spp. (Pholcidae), the most common prey item of *Stenolemus* in nature (Soley et al., 2011). When the bug entered the web, the spider ran to it and wrapped its head, antennae, and some legs (including its raptorial forelegs) with silk. The spider retreated momentarily, then renewed the attack. At this point the bug oriented one of its long hindlegs and repeatedly tapped toward the spider in a forceful way; one of these movements contacted (i.e., ‘kicked’) the leg of the spider, and caused the spider to retreat (see video at 10.6084/m9.figshare.14112974). As the spider retreated, the bug continued flexing its hind leg (see video at 10.6084/m9.figshare.14112974). Less than two minutes later, the spider attacked again while the bug was attempting to groom itself free of the entanglement. This time, the bug placed an untangled foreleg on the ground, and used it to pivot slightly to align itself facing partially away from the spider, and then delivered a single, strong tap with the same hind leg. This second kick was more precise, and involved only one leg thrust to strike the spider (see video at 10.6084/m9.figshare.14112974). The spider retreated and the bug eventually freed itself, and continued to stalk the spider for several hours before finally abandoning the web.

The only other instance in which kicking was observed was in an interaction between another adult female *S. giraffa* and a large *Trichocyclus* sp. The spider had wrapped the bug’s front legs with silk, retreated, then attacked again. The bug repeatedly flexed its right hind leg and contacted the spider once, but the spider continued its attack (see video at 10.6084/m9.figshare.14112974). Seconds later, the spider slowly retreated, and the bug suddenly swung the same leg forcefully toward the spider but without reaching it (video S1). The spider returned and attacked on several occasions while the bug groomed itself free. The bug did not kick in response to any of these subsequent attacks, and eventually groomed itself free and continued stalking the spider; after several hours it finally killed the spider.

Behaviours such as crouching or striking may be ‘last resort’ defence mechanisms (e.g., Bowers et al., 1993; Lourenço-de-Moraes et al., 2016) that have evolved as pre-programmed responses to a common problem: aggressive approaches by spiders (Soley & Taylor, 2013). However, the problem these two bugs faced (being attacked by their quarry and having their defensive forelegs, but not other legs, wrapped in silk) is rare: it was observed in only 2 of over 170 encounters with aggressive spiders in the field and lab (FGS, unpub.). This suggests that the bugs’ kicking behaviour might have been an insightful defensive innovation. Kicking was never observed in any other instance in which the spiders approached or attacked the bugs (Soley et al., 2011; Soley & Taylor, 2012, 2013); it only occurred in these rare instances in which the bugs had their forelegs wrapped in silk. Even though the bugs may possess general pre-programmed responses such as ‘tap with the leg’, insight may have been involved in using these behaviours in a new context. There are other possibilities, however. The predatory behaviour of early instars (1st-2nd instars) is poorly studied, and it is still possible that spider attacks are more frequent during these stages, so that behaviours such as kicking with the hind legs could offer a significant advantage and become part of the innate behavioural repertoire. We also cannot rule out learning. For instance, the behaviour may have occurred randomly (cf., Eberhard, 1990, 2000) earlier in the life of the bug, without the animal initially understanding its mechanical consequences, but resulting in spiders (or other enemies) retreating. We cannot dismiss these alternatives to insightful behaviour due to our lack of data on the bugs’ previous experiences, and because the context of spider attacks is not uncommon for these bugs.

Another possibility is that the bugs may have learned that striking at a spider with the front legs induced the spider to leave, and used insight to transfer this knowledge and achieve the same outcome through different means (kick with the hind leg). The possibility that innate motor routines associated with defensive strikes could be transferred in a pre-programmed way to other legs (similar to the long-known compensation for missing legs during walking in various insects; Wilson (1966) and references), seems unlikely because the bug’s fore and hind legs are morphologically distinct, move differently, and are used in different behaviours (i.e., forelegs are used mainly for breaking threads, grooming, and striking, and only occasionally to sustain the bug’s weight while in webs; hindlegs are mainly used for walking, and never for striking or breaking threads). Also, given the rarity of this context it seems unlikely that such pre-programed transfer could be favoured by selection.

4. Discussion

The animals in the above anecdotes found adaptive solutions to novel or at least very uncommon problems. The response in the golden-orb weaver cannot be explained as the result of pre-existing programs that evolved under selection, because the problem seems to be extremely uncommon in nature. Similarly, the context of assassin bugs having forelegs, but not hindlegs, wrapped in silk seems uncommon enough to justify doubt that selection has occurred for programmed responses, but missing data on early instars mean that pre-existing responses cannot be excluded with a similar level of confidence as that for the spider. For both cases, it is still possible that the motor patterns were randomly generated by the animal in response to the problem. But if this were the case, one would expect a variety of other motor patterns to have been also expressed. Instead, the motor routines were unique and confined to particular body parts that solved the task at once. Hence, it is possible that these motor outputs carried a sensory prediction similar to the 'forward models' of motor patterns that are regularly expressed in similar animals (see Webb, 2004). For neither case could we rule out learning, although the animals' responses suggested that the solution had not been perfected when the animal confronted the problem (e.g. compare movements of hind leg performed by the assassin bug in the first vs. second approach by the spider). In general, reservations of this sort regarding possible cases of 'insight' in other species will undoubtedly fall at different points along this continuum of relative confidence.

The pre-programmed hypothesis is appealing for explaining many types of arthropod behaviour. However, selection favouring the maintenance of a pre-programmed behaviour will be weak if the problem it solves is unusual in nature, or if other behaviours are sufficient for solving the problem. For instance, a hard-wired kicking response would need to compete against other already effective hard-wired responses such as striking, bucking and stridulating. The existence of generalized defensive behaviour that can effectively be deployed to solve unusual problems would lower the selective advantage of potentially new, fine-tuned behaviours that are tailored to particular, uncommon problems.

A provocative possibility is that commonly used behavioural patterns are hard-wired, while feats such as stimulus generalization or adjustments of hard-wired responses to fit unusual situations are accomplished by learning and by some degree of insight. The ability to perform insightful innovations would be selectively advantageous, and also increase the adaptive value of the hard-wired responses that are employed in these situations (Sol, 2009; Loukola et al., 2017; Perry & Chittka, 2019).

Our observations have an additional implication for understanding the evolution of behaviour. In classic formulations, the evolutionary origin of fine-tuned behaviour is thought to depend on appropriate mutations that produce pre-programmed patterns. Evolutionary origins could sometimes be due, however, to insightful innovation and/or reorganization of pre-existing behaviour patterns for use in a different context. Such changes could in turn expose to selection any existing genetic variation in the regulation of their expression (including the ability to make insightful modifications) (Sol, 2009). This selection could then result in evolutionary changes in gene frequencies (West-Eberhard, 2003). We hope that the observations and arguments here encourage further experiments inspired by natural problems to test hypotheses concerning the cognitive abilities of these and other arthropods.

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References

Alem, S., Perry, C.J., Zhu, X., Loukola, O.J., Ingraham, T., Søvik, E. & Chittka, L. (2016). Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect. — PLoS Biol. 14: e1002564.

Bowers, B.B., Bledsoe, A.E. & Burghardt, G.M. (1993). Responses to escalating predatory threat in garter and ribbon snakes (*Thamnophis*). — J. Comp. Psychol 107: 25-33.

Byrne, R.W. (2016). Evolving insight. — Oxford University Press, Oxford.

Cross, F.R., Carvell, G.E., Jackson, R.R. & Grace, R.C. (2020). Arthropod intelligence? The case for *Portia*. — Front. Psychol. 11: 568049.

Eberhard, W.G. (1990). Imprecision in the behavior of *Leptomorphus* sp. (Diptera, Mycetophilidae) and the evolutionary origin of new behavior patterns. — J. Insect Behav. 3: 327-357.

Eberhard, W.G. (2000). Breaking the mold: behavioral variation and evolutionary innovation in *Wendilgarda* spiders (Araneae Theridiosomatidae). — Ethol. Ecol. Evol. 12: 223-235.

Eberhard, W.G. (in press). Small details in a large spider: cheliceral and spinneret behavior when Trichonephila clavipes (Araneae: Araneidae) cuts lines and wraps prey. — J. Arachnol.

Fitzpatrick, S. (2008). Doing away with Morgan's Canon. — Mind Lang. 23: 224-246.

Heinrich, B. & Bugnyar, T. (2005). Test problem solving in ravens: string-pulling to reach food. — Ethology 111: 962-976.

Higgins, L. (1992). Developmental changes in barrier web structure under different levels of predation risk in *Nephila clavipes* (Araneae: Tegragnathidae). — J. Insect Behav. 5: 635-655.

Hingston, R.W.G. (1922). The snare of the giant wood spider (*Nephila maculata*). Part III. Further lessons of the *Nephila*. — J. Bombay Nat. Hist. Soc. 28: 917-923.

Jackson, R.R. & Cross, F.R. (2011). Spider cognition. — Adv. Insect Physiol. 41: 115-174.

Jacobs, I.F. & Osvath, M. (2015). The string-pulling paradigm in comparative psychology. — J. Comp. Psychol. 129: 89-120.

Logan, C.J., Avin, S., Boogert, N., Buskell, A., Cross, F.R., Currie, A., Jelbert, S., Lukas, D., Mares, R., Navarrete, A.F., Shigeno, S. & Montgomery, S.H. (2018). Beyond brain size: uncovering the neural correlates of behavioral and cognitive specialization. — Comp. Cogn. Behav. Rev. 13: 55-89.

Loukola, O.J., Perry, C.J., Coscos, L. & Chittka, L. (2017). Bumblebees show cognitive flexibility by improving on an observed complex behavior. — Science 355: 833-836.

Lourenço-de-Moraes, R., Ferreira, R.B., Mira-Mendes, C.V., Zocca, C.Z., Medeiros, T., Ruas, D.S. & Solé, M. (2016). Escalated antipredator mechanisms of two Neotropical marsupial treefrogs. — Herpetol. J. 26: 237-244.

Morgan, C.L. (1894). An introduction to comparative psychology. — Walter Scott, London.

Perry, C.J. & Chittka, L. (2019). How foresight might support the behavioral flexibility of arthropods. — Curr. Opin. Neurobiol. 54: 171-177.

Perry, C.J., Barron, A.B. & Chittka, L. (2017). The frontiers of insect cognition. — Curr. Opin. Behav. Sci. 16: 111-118.

Robinson, M.H. & Mirick, H. (1971). The predatory behavior of the golden-web spider *Nephila clavipes* (Araneae: Araneidae). — Psyche 78: 123-139.

Robinson, M.H. & Robinson, B. (1973). Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. — Sm. C. Zool. 149: 1-76.

Robinson, M.H., Mirick, H. & Turner, O. (1969). The predatory behavior of some araneid spiders and the origin of immobilization wrapping. — Psyche 76: 487-501.

Shettleworh, S.J. (2010). Cognition, evolution, and behavior. — Oxford University Press, Oxford.

Shettleworth, S.J. (2012). Do animals have insight, and what is insight anyway? — Can. J. Exp. Psychol. 66: 217-226.

Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. — Biol. Lett. 5: 130-133.

Soley, F.G. (2016). Fine-scale analysis of an assassin bug's behaviour: predatory strategies to bypass the sensory systems of prey. — Roy. Soc. Open Sci. 3(10): 160573.

Soley, F.G. & Taylor, P.W. (2012). Araneophagic assassin bugs choose routes that minimize risk of detection by web-building spiders. — Anim. Behav. 84: 315-321.

Soley, F.G. & Taylor, P.W. (2013). Ploys and counterploys of assassin bugs and their dangerous spider prey. — Behaviour 150: 397-429.

Soley, F.G., Jackson, R.R. & Taylor, P.W. (2011). Biology of *Stenolemus giraffa* (Hemiptera: Reduviidae), a web invading, araneophagic assassin bug from Australia. — New Zeal. J. Zool. 38: 297-316.

Webb, B. (2004). Neural mechanisms for prediction: do insects have forward models? — Trends Neurosci. 27: 278-282.

Weirauch, C., Forero, D. & Jacobs, D.H. (2011). On the evolution of raptorial legs — an insect example (Hemiptera: Reduviidae: Phymatinae). — Cladistics 27: 138-149.

West-Eberhard, M.J. (2003). Developmental plasticity and evolution. — Oxford University Press, Oxford.

Wilson, D.M. (1966). Insect walking. — Annu. Rev. Entomol. 11: 103-122.

Zentall, T.R. (2018). Morgan's canon: is it still a useful rule of thumb? — Ethology 124: 449-457.