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SHORT COMMUNICATION

Portia's capacity to decide whether a detour is necessary

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ABSTRACT

Proficiency at planning is known to be part of the exceptionally complex predatory repertoire of *Portia*, a genus of jumping spiders (Salticidae) that specialize in preying on other spiders. This includes proficiency at choosing between two detour routes, with only one leading to otherwise inaccessible prey. Less is known about *Portia*'s proficiency at making strategic decisions pertaining to whether a detour is required or not. Using *Portia africana*, we investigated this by having lures (prey or leaf pieces) visible at the beginning of a trial but not later, and by using water to restrict *P. africana*'s freedom of movement. A detour path was always present, but sometimes a causeway was also present, allowing direct access to lures. After seeing prey, *P. africana* more often took the causeway when present and, when absent, more often took the detour path. After seeing leaf pieces, *P. africana* never took the detour path.

KEY WORDS: Cognition, Detouring, Planning, Representation, Spider, *Portia africana*

INTRODUCTION

In casual language, 'cognition' is associated with the term 'thinking' and, in this context, there tends to be exceptional interest in examples of animals relying on plans. Geffner (2013) proposed three basic ways by which an individual might make plans, with these ways being aligned with Dennett's (1996) distinctions between Darwinian, Skinnerian and Popperian creatures. A Darwinian creature relies on what Geffner (2013) called a 'hard-wired approach', with the animal's 'innate' or 'instinctive' (Lorenz, 1965) plan being derived by natural selection, a trial-and-error process acting over evolutionary time (Mayr, 1982). By practising trial-and-error in its own lifetime, a Skinnerian animal is more plastic in the way it adjusts to its environment (Enquist et al., 2016). However, in the context of animal cognition, Popperian creatures are particularly interesting because, instead of solving problems by physically acting in the environment in real time, these creatures derive solutions to problems ahead of time by formulating plans and then acting on those plans. Geffner (2013) characterized planning by Popperian creatures as 'thinking before acting' (p. 341) and as using a 'model-based approach to action selection' (p. 342). Instead of calling this a 'model-based approach', we prefer to characterize planning by Popperian creatures as reliance on an internal representation of the problem at hand when formulating and executing plans. Following Burge (2010) and Hogan

(2017), we envisage this style of reliance on representation as being instances of crossing a threshold into the realm of genuine cognition.

Our specific interest in Popperian creatures has come especially from research on *Portia* (Jackson and Cross, 2011), a genus of jumping spiders (Salticidae). Salticids have unique, complex eyes and an exceptional ability for seeing detail in visual objects (Harland et al., 2012). Although many salticids prey primarily on insects (Jackson and Pollard, 1996), *Portia* is a web-invading predator that uses a wide variety of different prey-specific prey-capture tactics for targeting other spiders as preferred prey (Jackson and Cross, 2013). Sometimes *Portia*'s prey-capture strategy in the field includes proficiency at gaining access to spiders in webs by following indirect paths (i.e. detours; Jackson and Wilcox, 1993). The first experimental evidence of *Portia*'s capacity to plan detours ahead of time came from using apparatus in which a particular species, *Portia fimbriata*, could view two detour routes, with only one leading to prey. Even when accessing this route required first moving directly away from the prey ('reversed-route detour'; see Tarsitano and Jackson, 1994) and even when the prey was no longer in view during the journey (Tarsitano and Jackson, 1997), *Portia* was proficient at identifying and then following the correct detour.

In a later study (Cross and Jackson, 2016), another five *Portia* species plus nine spider-eating salticid species from other genera were used in detouring experiments, with each trial beginning with a salticid at the top of a tower and with prey lures in view at the end of only one of two walkways. After walking down from the tower, these salticids consistently went to the beginning of the walkway leading to the prey. No shortcuts were available because the prey were outside the salticid's jumping range and the supports for the walkways were situated in a pan of water, exploiting these salticids' aversion to getting wet (Cross and Jackson, 2015).

However, in field observations of *Portia*'s detouring behaviour (e.g. Jackson, 1992), the most basic decision *Portia* appeared to make did not pertain to choosing between two detour routes where only one led to prey, but rather pertained to whether *Portia* took a detour route instead of a direct route, where both routes led to prey. With this as our rationale, our objective here was to investigate *Portia*'s proficiency at deciding ahead of time whether to take a long winding path to reach the prey.

MATERIALS AND METHODS
General

Test subjects were F2-generation juveniles (body length, 4.0 mm) of *Portia africana* (Simon 1886) (hereafter *P. africana* or 'test spider') from laboratory cultures. The experimental prey were lures made from adult females (body length, 3.0 mm) of *Oecobius amboseli* Shear & Benoit 1974 (Oecobiidae; hereafter *O. amboseli* or 'oecobiid'). This spider species, which is often aggregated in the field, is a common natural prey of *P. africana* (Jackson and Nelson, 2012). For *P. africana*'s maintenance diet in the laboratory, we used a variety of spiders that do not, to human observers, bear especially close resemblance to oecobiids: the juveniles (size similar to oecobiids) of *Argyrodes* Simon 1864 (Theridiidae), *Leucauge* White 1841

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(Tetragnathidae), *Nephilengys* L. Koch 1872 (Nephilidae) and *Pardosa* C. L. Koch 1833 (Lycosidae). *Oecobius amboseli* and the maintenance prey were collected from the field as needed. Test spiders had no prior experience with oecobiids, the experimental apparatus or any other apparatus that required taking a detour or avoiding water. No test spider was used in more than one trial or moulted sooner than 7 days after a trial, and each had moulted 7–10 days before being used in a trial. All relevant permits were covered by our Visiting Scientist contracts with the International Centre of Insect Physiology and Ecology (ICIPE).

Apparatus

The apparatus (Fig. 1) consisted of a primary platform (120×100 mm) that was glued (Dolphin 140 General Purpose Silicone Sealant) to the floor of a water-filled pan (495×210 mm), a tower (height 100 mm, diameter 20 mm) situated on top of the primary platform, a pit (depth 10 mm, diameter 10 mm, covered by a lid) centred on the top of the tower, a display platform (130×50 mm) that was surrounded by water on three sides, with a 30 mm high wall on those three sides (the other side was against the pan wall), a display box (100×40 mm, 6 mm high wall on three sides, with the other side against the pan wall) situated behind the wall on the display platform, and a single walkway (width 10 mm) that went indirectly from the primary platform to the display platform (length of segments 1–3: 120, 100 and 95 mm, respectively). A causeway (100×40 mm, Fig. 1A) was also sometimes present between the primary platform and the display platform.

The water in the pan was almost level with the top of the primary platform, display platform, walkway and causeway. The front edge of the tower was 10 mm from the end of the primary platform closest to the display box ('front side'), and the walkway began midway on the

right-hand side (when facing the scene) of the primary platform ('walkway beginning'). All components of the apparatus were made from 2 mm thick opaque, non-reflective glass. In basic respects, this and the water-based apparatus used previously (Cross and Jackson, 2016) were similar, with the most important differences being that here there was only one indirect path (walkway), instead of two, and a causeway, which, when in place, became a direct, dry path to the prey.

Before each trial began, the lid confined the test spider to the pit for 10–15 min. The lid was then lifted away so that the test spider could walk out on to the top of the tower and view the scene in the display box. In experimental trials, there was a prey scene made from nine lures. In control trials, there was a control scene made from nine dead (dry, brown) *Lantana camara* leaf pieces. The leaf pieces were circles of about the same size as the oecobiids, and we chose brown leaves because this leaf colour was similar to the colour of *O. amboseli*. The oecobiids or leaf pieces were evenly arranged in the display box in two rows, with five in the first row and four in the second (see Fig. 1, inset).

The oecobiids were preserved in 80% ethanol and were removed from the ethanol and allowed to dry on the day before they were used. Each oecobiid and each leaf piece was glued to the centre of the upper surface of a cork disc (10 mm diameter, 2 mm thick) using sticky gum (Tanglefoot® Pest Barrier). Each lure was then secured with sticky tape to the floor of the display box and, to hold the oecobiids or leaf pieces firmly in place, each scene was sprayed with a transparent plastic adhesive (Crystal Clear Lacquer, Atsco Australia Pty, Cheltenham, VIC, Australia). As test spiders were prevented from contacting scenes during trials, the same prey scene was used in all experimental trials and the same control scene was used in all control trials. Between trials, each scene was kept in an airtight plastic box in a refrigerator.
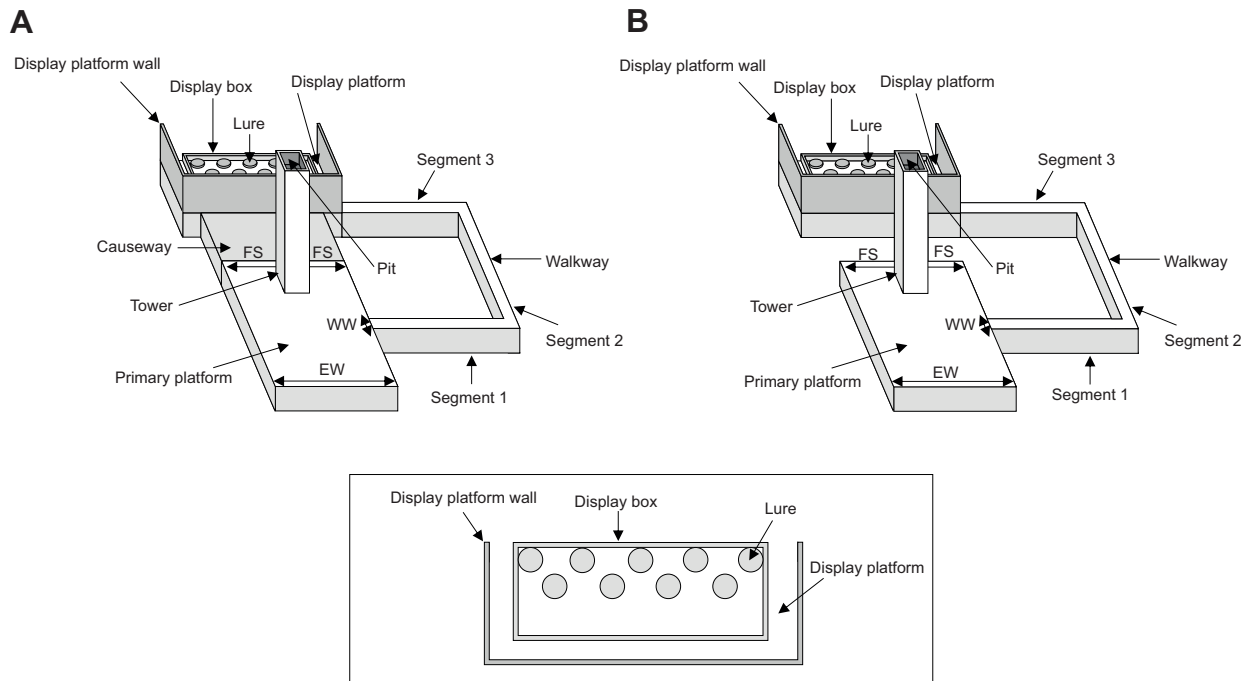

Fig. 1. Experimental apparatus. (A) Causeway present; (B) causeway absent. The tower was positioned on the primary platform; the pit on top of the tower held the test spider before the trial began (lid not shown). The display box was located on the display platform, surrounded on three sides by the display platform wall, which hid the lures or leaf pieces from view when the test spider moved off the tower. The walkway (WW: walkway beginning) provided an indirect path from the primary platform to the display platform. When present, the causeway filled the space between the display platform and the front side (FS) of the primary platform. The exit wall (EW) gave the test spider a way to opt out of the trial. The apparatus was placed in a water-filled pan (not shown) with surrounding walls. Experimental trials: nine lures made from *Oecobius amboseli* (inset: arrangement of lures in the display box, when viewed from above). Control trials: nine dry, dead leaf pieces from *Lantana camara*. Drawings not to scale.

If there were any oecobiid odours that *P. africana* might have detected, then it is likely that the ethanol removed it. However, preservation, not removal of odour, was the rationale for using the ethanol. There was no need to preserve the leaves because there was no noticeable decay or mould during the period of their use.

The display platform wall ensured that the test spider could not view the scene after leaving the tower. When the causeway was in place, the test spider could go straight to this wall from the bottom of the tower. Alternatively, it could gain indirect access to the display platform by moving directly away from the display platform to reach the beginning of the walkway. In the absence of the causeway, the walkway was the test spider's only means of accessing the display platform without getting wet.

Four glass walls surrounded the pan (495 mm×210 mm), three being 200 mm high and the fourth being only 40 mm high. The shorter wall was called the 'exit wall' because it was in contact with the primary platform at the end opposite the display platform, giving test spiders a way to leave the primary platform without taking the walkway or the causeway and without getting wet.

Procedure

Our criteria for accepting trials as successful corresponded to the criteria in the earlier water-based experiments (Cross and Jackson, 2016). Whenever one of these criteria was violated, we ended the trial and did not use the test spider again, but fewer than 20% of trials for either treatment were unsuccessful.

A successful trial began when the test spider left the pit within 10 min and then stood on top of the tower for at least 10 min. From the top of the tower, the lures, display platform, walkway, causeway (if present), pan and walls of the pan were all potentially in the spider's line of sight. Before leaving the top of the tower in a successful trial, the test spider had to spend a total of at least 240 s fixating its gaze on the critical parts of the scene (i.e. the display box, each segment of the walkway, the front side of the primary platform where the causeway, if present, began, or where the beginning of the causeway would have been if present), where 'gaze fixation' is defined as in earlier studies (Tarsitano and Andrew, 1999; Cross and Jackson, 2016) as instances of the spider having its large forward-facing principal eyes oriented towards the specified components of the apparatus. For a trial to be successful, no more than 60 min could elapse between the test spider leaving the pit and walking off the top of the tower, and then, before another 5 min elapsed, the test spider had to arrive on the primary platform. Another requirement for a successful trial was that, from the tower, test spiders did not leap into the water or on to the primary platform and, after leaving the tower, they did not leap into the water surrounding the primary platform. Yet another rule was that, whenever the test spider chose the exit wall, the trial was recorded as unsuccessful.

Each successful trial ended when a test spider chose the front side or the walkway beginning, with our operational definition of 'choose' being that the spider stepped on to one of these parts of the apparatus. However, we also recorded whether the spider proceeded from the causeway or walkway and subsequently arrived at the display platform within the following 45 min without 'doubling back'. Doubling back refers to instances of the test spider, while on the causeway or the first segment on the walkway, moving back to the primary platform and then failing to return to its current location within 30 s. Doubling back also refers to instances of the test spider, while on the walkway, moving from its current location back to a previously visited segment and then failing to return to its current location within 30 s. Our rationale for excluding instances of

doubling back was to minimize the test spider's opportunities to alter plans made while on the tower.

Our primary interest was whether *P. africana* planned where to go while it was still on top of the tower. As another means of minimizing the test spider's opportunities to alter plans made while on the tower, we only recorded a trial outcome as being an instance of a test spider choosing the walkway or the front side when these were approached directly. By 'direct', we mean that the test spider never moved more than 20 mm away from the front side and then doubled back, or never moved 20 mm past the beginning of the walkway and then doubled back. 'Direct' also meant that, while en route to the front side or the walkway beginning, the test spider never oriented its gaze 45 deg or more from the front side or from the walkway beginning for more than 60 s. This direct-approach requirement was adopted partly because we wanted to minimize *P. africana*'s opportunities for viewing the full extent of its surroundings while on the primary platform after leaving the tower. Another reason was that we wanted to minimize variation in the paths that the test spider took, as well as instances of it simply arriving at the front side or walkway beginning by chance. This, in turn, simplified our data analysis (see below) and made the conclusions more straightforward.

Test spiders had no opportunity to touch the display box or any of the lures because we ended trials and removed test spiders from the apparatus as soon as they reached the display platform wall. Knowing that *P. africana* responds to chemical stimuli from conspecific individuals (Nelson et al., 2012), we cleaned the apparatus with ethanol and distilled water, and replaced the water in the pan after each trial. These procedures, as well as our decision to use apparatus made of glass, minimized the possibility of contact-chemical traces from earlier trials influencing experimental outcomes.

All trials were conducted between 08:00 h and 14:00 h (laboratory photoperiod, 12 h light:12 h dark, lights on at 07:00 h). For standardizing hunger level and for confirming that test spiders were motivated to respond to lures, all test spiders were kept on a 7 day fast immediately before testing and, after each successful trial, the test spider was given access to living prey (three oecobiids put into a plastic cage with the test spider) at 15:00 h on the same day as the trial; all test spiders captured the prey before 60 min elapsed.

Data analysis

We continued experimental trials until we had data from 60 successful trials with the causeway present and another 60 with the causeway absent. As few of the control trials were successful, we continued until 24 spiders made a choice with the causeway present and 25 with the causeway absent, with these data for control trials including spiders that chose the exit wall.

For a general overview of our results, we first used a nominal logistic regression where we included trial type (experimental or control) and causeway (present or absent), plus their interaction, as factors in the model, and where we used the choices made during the experiment (for front side, walkway or exit wall) as the dependent variable. The logistic regression revealed significant effects of both the trial type and causeway, but no evidence of a significant interaction between the two.

We then used chi-square tests of independence to specifically compare the number of spiders that chose the walkway beginning in experimental and control trials, the number of spiders that chose the walkway beginning when the causeway was present or absent (analysed for spiders in experimental trials only), and the number of spiders that chose the exit wall when the causeway was present or absent (analysed separately for spiders in experimental and control

trials). We also compared, for spiders in experimental trials, the number that completed the walkway when the causeway was present and when it was absent. To analyse data, we used SAS JMP 14 and Statistica 13. For more details on statistical methods, see Howell (2002).

RESULTS AND DISCUSSION

The overall nominal logistic regression model was significant (χ^2=93.38, P<0.001). Wald tests revealed significant effects of both trial type (χ^2=16.16, P<0.001) and presence/absence of the causeway (χ^2=14.42, P<0.001), but there was no evidence of a significant interaction between these factors (χ^2=1.59, P=0.452).

We then looked more closely at the data using chi-square tests of independence. In experimental trials, 49 spiders chose the walkway beginning and 92 made other choices; by comparison, in control trials, none chose the walkway beginning and 49 made other choices (χ^2=22.95, P<0.001; Table 1). This result is consistent with prey being salient to *P. africana* when choosing a route.

We found evidence that whether the causeway was present or absent during experimental trials influenced the test spider's choice. Most (38 out of 60) chose the walkway beginning when the causeway was absent but, when the causeway was present, most (49 out of 60) chose the front side (χ^2=25.15, P<0.001). These findings suggest that *P. africana* normally takes an indirect route when no direct route can be seen and, when available, takes a shorter, direct route.

We also found no evidence of the presence–absence of the causeway influencing whether test spiders completed the path from the beginning of the walkway to the display platform (χ^2=0.75, P=0.387; Table 1) and this suggests that route choice is the test spider's primary decision. It seems that, after reaching the walkway beginning, test spiders simply followed the walkway despite no lures now being visible.

One of the most striking findings from this study is that test spiders never chose the walkway during control trials when leaf pieces instead of prey were visible from the tower. Yet, even when the causeway was present, test spiders sometimes went to the walkway beginning specifically when they could view prey. This suggests that, while on the tower, *P. africana* determined by sight whether the display box held relevant objects (namely prey) instead of irrelevant objects (namely leaf pieces) and, on this basis, made a decision about taking the walkway.

In control trials, many test spiders chose the exit wall instead of the front side, and whether this happened was influenced by whether the causeway was present. When the causeway was present, 15 chose the front side and nine chose the exit wall; however, when the causeway was absent, only four test spiders chose the front side, with the other 21 choosing the exit wall (χ^2=11.15, P<0.001). This suggests that, during control trials, test spiders were choosing the causeway as an alternative way of leaving the apparatus. By contrast,

there was no comparable effect of causeway presence–absence on test spiders choosing the exit wall during experimental trials, which is consistent with test spiders making decisions about accessing prey. When the causeway was present in these trials, 60 chose the front side or walkway and nine chose the exit wall; when the causeway was absent, 60 chose the front side or walkway and 12 chose the exit wall (χ^2=0.36, P=0.546).

As a way to guard against premature, de facto conclusions about cognition, we use the expression 'detouring' simply for instances of animals following indirect paths. This precaution is important because, despite the shared term, the research on detouring by salticids seems to address questions only moderately aligned to much of the research on detouring by larger animals, such as octopus, turtles, dogs and cats (Kabadayi et al., 2018). For example, the experimental design used with larger animals has often included a see-through barrier made of glass or wire between the test subject and a target (e.g. food) and, typically, test subjects repeatedly make unsuccessful attempts to move straight ahead. Success in these experiments tends to be achieved only when the test subject terminates its futile efforts to go straight ahead and instead walks around the barrier, making it easy to suggest that the test subject has suddenly understood how to reach the target stimulus. This, in turn, suggests that the test subject had to overcome a strong initial inclination to move straight toward a goal. In these experiments, the detour problem can also be appropriately referred to as an impulse-control problem where 'impulse control' (or 'self-control') is a convenient expression for instances of animals inhibiting a prepotent response to seeing the target (Beran, 2015).

Yet, for *P. africana* in our experiments, there was little to suggest that impulse control was particularly relevant. Although 22 individuals chose the front side when prey were present and the causeway was absent, significantly more chose the walkway instead. Moreover, our findings did not come from spiders eventually taking a detour after repeated failed attempts to go straight to the prey. There was only one trial for each test spider, and most chose the walkway (i.e. the detour path) when this was the only way to reach the prey. While on the tower, these individuals seemed to purposefully go about the business of assessing the situation, planning how to reach a desired destination, and then acting on the plan. Rather than showing dog-like impulsiveness (see Tarsitano and Andrew, 1999; Chang et al., 2018), they instead appeared to be poised and ready to solve a problem requiring planning.

The problem presented to *P. africana* in the present study, however, differed from the detour problems in Tarsitano and Jackson (1997) and Cross and Jackson (2016) where taking a lengthy detour was the only way to reach the prey. In the present study, *P. africana* was instead faced with the problem of deciding whether a detour was necessary; typically, *P. africana* took the detour when necessary and took the direct path when it was available and led to prey. It was rare for *P. africana* to leap straight from the tower toward the prey.

The problem we presented to *P. africana* here also differed from the problem presented to *Portia occidentalis* (formerly *P. labiata*) in experiments in which the prey was *Scytodes pallida* and the choice for *P. occidentalis* was between going directly (i.e. straight ahead) toward a facing prey individual or approaching it from behind (Jackson et al., 2002). This prey species is from the family Scytodidae and, for *Portia*, scytodids are especially dangerous because, from their chelicerae, they spit a sticky gum over their own prey as well as over would-be predators like *Portia* (Li et al., 1999). Maternal scytodid females are a relatively safe type of prey because they hold on to their eggs with their chelicerae, which means they

Table 1. The number of test spiders that chose the front side (FS) of the primary platform, walkway beginning (WW) or exit wall (EW) when the causeway was present or absent

Trial	Causeway	Chose FS	Chose WW	Chose EW
Experimental	Present	49 (41)	11 (2)	9
	Absent	22 (N/A)	38 (12)	12
Control	Present	15 (13)	0 (N/A)	9
	Absent	4 (N/A)	0 (N/A)	21

The number of test spiders that, having made their choice, completed the journey across the causeway or walkway is given in parentheses.

have to let go of their eggs before spitting. In experiments, *P. occidentalis* usually approached the egg-carrying scytodids directly and, by taking a detour, approached eggless scytodid females from behind (Jackson et al., 2002).

In the *P. occidentalis*–scytodid experiments (Jackson et al., 2002), *P. occidentalis*' problem can be envisaged as pertaining primarily to safety and, during each trial, a direct as well as an indirect path was always available. Using oecobiids, *P. africana*'s problem in the present study can be envisaged rather differently. Unlike scytodids, oecobiids are not a particularly dangerous prey for *Portia*. Another difference is that the scytodid remained in view during trials in the earlier study, but here *P. africana* had no opportunity to see the oecobiids again after initially viewing them, and the detours taken by *P. africana* in the present study were considerably longer than those in the *P. occidentalis*–scytodid experiments. As yet another difference, there was no water barrier in the apparatus used for the *P. occidentalis*–scytodid experiments, but here the apparatus sat in a pan of water and *P. occidentalis* apparently made decisions partly on the basis of detecting the presence of water. However, the primary way the present study differed from the *P. occidentalis*–scytodid experiments is that here, instead of making decisions primarily on the basis of safety, *P. africana* made decisions pertaining to whether or not a direct path was available.

The results in the current study, as well as in other detouring-related research, suggest that *Portia*, as a Popperian creature, makes strategic detouring decisions ahead of time. Moreover, *Portia*'s capacity for making plans is not unique to detouring and is, instead, expressed in a variety of other contexts as well (e.g. Jackson and Cross, 2013). Of course, a spider brain sitting next to the brain of a primate will seem pathetically tiny, but even when discussing a mere spider there is no need to make the kind of overly liberal use of 'cognitive' (e.g. Stewart, 1995) that tends to erode the association of 'cognitive' with the concept of Popperian creatures. For instance, the converging evidence of *Portia*'s capacity to make plans is out of step with the notion of *Portia* compensating for small brain size by using simple rules to solve a detouring task (e.g. Barrett, 2011) or by relying on 'extended cognition' (Japyassú and Laland, 2017) as a way to by-pass the need for internal representation (Cheng, 2018).

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