

Article

Distance assessment of detours by jumping spiders

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Abstract

To take an indirect route (detour) in order to reach a specific target requires complex cognitive processes. Yet more demanding, from the cognitive point of view, is when the goal is only visible at the beginning of the detour. In spiders from the family Salticidae, vision is a key sensory modality mediating navigation and prey search. Their acute vision allows them to perform complicated detours, possibly as a consequence of the multitude of potential routes in their typically complex 3-dimensional habitats. We used a 4-route choice test, in which routes differed in being either short or long and in the presence or absence of a lure of a prey item, to investigate route assessment in 2 salticid species, *Trite planiceps* and *Marpissa marina*. Although both species showed evidence of motivation to follow lured-routes, judging by the number of times they re-oriented toward them while detouring, we found that *Trite* chose short routes in preference to long routes, but did not prefer the lured-routes. In contrast, *Marpissa* exhibited random route choice, although it oriented toward lured-routes more often than control routes (lure absent). Our results suggest that decision-making processes about which route to take occurs before embarking on a route, but this is cognitively challenging. Spiders exhibited cognitive limitations in which the lack of visibility of the goal affected success. However, the severity of cognitive limitations depended on species. We suggest that variability in spatial ability across the Salticidae may be related to the habitat complexity inhabited by each species.

Key words: cognition, cognitive limitations, decision-making, detour behavior, Salticidae, spatial task

The cognitively simple process of moving in a straight line toward a visualized goal occurs as an instinctive response (Köhler 1927). However, using an indirect route to reach a goal (detouring) requires mental operations beyond innate responses, such as different types of learning and disruption/retention mechanisms (Kabadayi et al. 2018). Even more complexity is required when the goal becomes invisible while the individual executes the detour. In this case, without the use of cues emanating from the goal, the subjects rely on working memory, route planning, and orientation (Wells 1967; Cross and Jackson 2016). The latter detours can be performed by vertebrates (Regolin et al. 1995; Zucca et al. 2005), and also by invertebrates with outstanding eyesight, such as octopuses (Wells

1970) and jumping spiders (Araneae: Salticidae) (Cross and Jackson 2016). Salticids are characterized by their highly acute vision (Land 1969; Harland et al. 2011) based on a visual system comprised of one pair of principal eyes and 3 pairs of secondary eyes. The principal, or anterior medial eyes (AMEs), are crucial for high spatial acuity and color vision, whereas the secondary eyes can detect motion over about 360° surrounding the spider (Harland et al. 2011).

In salticids, vision is a key sensory modality mediating prey capture (Jackson 2000; Li et al. 2003), agonistic displays (Wells 1988; Taylor et al. 2001), visual courtship (Clark and Morjan 2001), and navigation (Hoefler and Jakob 2006). When foraging, salticids visually identify their prey at a distance (Richman and Jackson 1992)

and stalk prey using a readily observable set of behaviors: the spider initially orients its cephalothorax toward the prey with the AME facing it—a behavior known as “orientation,” after which, if prey is identified, the salticid slowly approaches and finally catches it by pouncing from 2 to 3 cm (Forster 1977). When a direct route to reach a visually located prey is not available, salticids may perform detours (Punzo 2004; Jakob et al. 2011). Detouring implies route planning (Cheng 2016) and spatial learning or ability (Thorpe 1963; Healy 1995). Scanning behavior, in which salticids systematically move their cephalothorax and body to inspect their surroundings using their AME, precedes detours, and is believed to be crucial for a priori-based route selection (Tarsitano and Andrew 1999; Cross and Jackson 2016). However, while detouring, salticids may not always see the goal, and may rely on spatial memory or on an internal representation of the prey’s relative position (Hill 1979; Tarsitano and Jackson 1992; Tarsitano and Andrew 1999; Tarsitano 2006). During a detour, salticids often “re-orient” toward the location of the goal in order to keep track of it (Hill 1979). Such re-orientations allow the spider to readjust its detour or stop detouring if the goal (e.g., prey) moves to another location. Detours are represented by a sub-goal (e.g., leaf or branch), or a series of sub-goals, that spiders need to initially reach to enable access to the main goal. Hence, using detours implies making associations of sub-goals that will lead to the primary objective. Hill (2007) suggested that salticids can use tertiary and possibly quaternary objectives depending on the length and complexity of the detour.

Commonly living in complex 3-dimensional environments, salticids are likely to encounter several possible detours that may or may not lead to a desired goal. Thus, decision-making becomes essential from an adaptive point of view (Punzo 2000), as choosing the most efficient route (the one that leads to prey, the shortest, the safest, etc.) allows the spider to save time and energy, and to be less vulnerable to predators (Gibson et al. 2007). Several salticid species have been shown to take detours (Hill 1979; Tarsitano and Jackson 1992, 1994; Carducci and Jakob 2000; Cross and Jackson 2016), suggesting this to be a common behavior in this family. Previous studies about detour assessment in salticids have focused on testing spatial abilities of species in the subfamily Spartaeninae (Jackson and Wilcox 1993; Tarsitano and Jackson 1994), and the majority of these studies provide 2 alternate detours (one detour leading to prey and a no-prey control; Tarsitano and Jackson 1992, 1997; Tarsitano 2006; Cross and Jackson 2016). However, detour assessment combining length and the presence of prey as factors has not yet been tested. We tested this using a 4-choice test with 2 long and 2 short routes, with a prey lure on one of the long and on one of the short routes. Using 2 species of salticids from the Salticoida subgroup, *Marpissa marina* Goyen and *Trite planiceps* Simon, we wanted to determine: (1) if salticids are able to decide on a route during the scanning phase before embarking on a route, and remember this even after the goal is visually blocked; (2) if salticids prefer short routes over long routes; and (3) if there are species-specific differences in spatial ability.

As salticids can follow a secondary objective while apparently memorizing the spatial location of the goal (Hill 1979), we predicted that the spiders would reach the goal even if they could only see it at the beginning of the task. We also expected that salticids would choose the short route leading to prey compared with the other 3 routes; this being the most efficient route to a goal. It is known that closely related species can differ in spatial ability as a consequence of the environment in which they live (Kasumovic et al. 2013) because the environment can directly affect cognitive (van Praag et al.

2000) and spatial abilities (Parker and Gibson 1977; Striedter 2005; Park and Bell 2010). Consequently, we expected *Trite* to outperform *Marpissa*, because it inhabits a 3-dimensionally more complex habitat.

Materials and Methods

Test animals

All animals were collected in Canterbury, New Zealand. Experiments were carried out from 08:00 to 13:00 h in the laboratory at the University of Canterbury. *Trite planiceps* is a large (6–13 mm) salticid endemic to New Zealand and is typically found in coastal areas where it inhabits the rolled-up flax leaves of *Phormium tenax* and *Cordyline* spp. (Forster 1979). *Trite* were field-collected in Christchurch and were transferred to the laboratory, where they were housed individually in 1-L transparent plastic containers. Individuals were held in captivity for at least 1 week before testing. Water supply was available through a cotton wick submerged in water which protruded into the container. Spiders were fed weekly with 2 adult *Musca domestica*. Hunger level during testing was standardized by performing the tests 5–7 days after their previous meal, thus ensuring similar hunger levels between individuals.

Marpissa marina is native to the South Island of New Zealand. It lives in quite flat rocky shores and makes nests 2–6 m above the high tide mark (Vink and McQuillan 2015). Adult males are 5–8 mm and females 6–9 mm in body length, and subadults are typically about 1 mm smaller than adults. Collected individuals were housed and maintained as described for *Trite*.

Experimental setup

We exposed spiders to 4 different routes from which to choose in order to reach a prey (i.e., lure made from a dead fly on the goal platform, described below). To determine if spiders were able to evaluate, or cared about, the distance of the route to reach a prey, the routes were either long or short. Additionally, to identify if spiders were actually following a route because of the prey rather than as a consequence of random choice, the goal platforms at the end of each route either did, or did not, have prey. Thus, the 4 different routes were: (1) short-lured route; (2) long-lured route; (3) short-control route; (4) long-control route. We tested 53 *Trite* (23 females, 16 males, and 14 subadults) and 63 *Marpissa* (25 females, 19 males, and 19 subadults).

The arena (see Figure 1 for dimensions) consisted of an aluminum tray with a central starting platform (a wooden dowel) on which the spider was placed at the beginning of every trial. Surrounding the starting platform there were 4 routes made of articulated plastic sections (each 2.5 cm long) with magnetic bases. Short routes had 10 articulated sections (25 cm) and the long routes had 22 sections (55 cm). The distance from the starting platform to the goal platform on a long route was 114 cm, and 84 cm for short routes. All goal platforms were at the same height (20 cm) and distance (17 cm) from the starting platform, with the route bases being 30 cm from the base of the starting platform. Consequently, the spider could see the 4 goal platforms at the same distance and height from the starting platform. External visual cues were blocked by black screens and the corner wall of the laboratory.

Goal platforms consisted of a square plate (4 × 4 cm) of aluminum with an attached “jiggler.” The jiggler allowed 5 Hz movement of a rigid wire (15° to each side of the vertical for 2 s; Dolev and

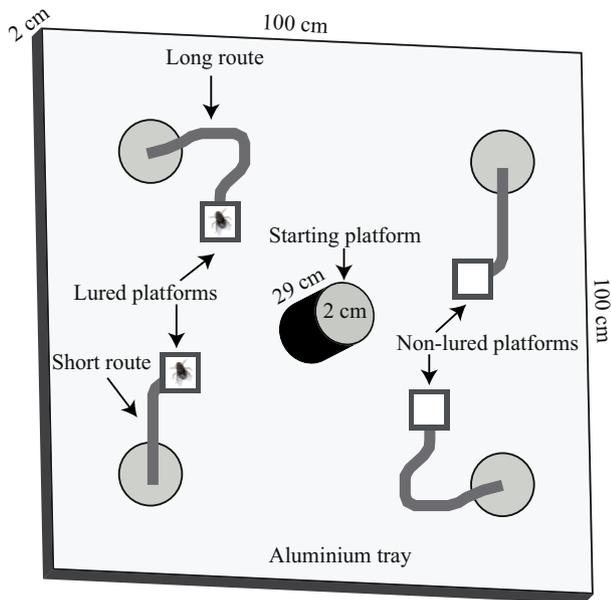


Figure 1. Aerial view of experimental arena (not to scale). To begin a test, spiders were placed on the starting platform from which they observed the 4 different routes to goal platforms with or without dead prey (lures).

Nelson 2016) to simulate prey movement when a lure was stuck on the wire. In control route goal platforms, this was comprised by the wire and a thin (1 mm) disc of cork, while in prey goal platforms, a dead prey on a thin cork disc was attached to the wire. Lures were adults of *Musca domestica* attached to the cork disc in a lifelike position and covered with transparent aerosol plastic adhesive (Jackson and Cross 2015). Jiggler movement, which serves to maintain the spider's attention, was activated only when the spider was facing a goal platform and any movement was stopped when the spider left the starting platform.

Spiders were placed on the starting platform in the center of the arena to begin a test. This allowed them to visually scan their surroundings to identify a goal, as once the spiders left the starting platform toward the base of the arena, visual cues on the goal platforms were no longer visible to test spiders. To eliminate directional bias, we randomly rotated the arena in 1 of 4 locations (North, South, East, and West). The position of the lures with respect to the routes (lure configuration) was also randomized for every trial. Consequently, each spider was exposed to one cardinal location plus one lure configuration. Each trial lasted 20 min, or less if the spider reached the lure; exceptions occurred when 20 min elapsed but the spider had started climbing one route. In these cases, trials ran until the salticid reached the end of the route or until it jumped off the route. However, if 20 min had elapsed and spiders had not left the starting platform or if the spider reached the edge of the arena, the spider was re-tested the next day. The arena was wiped with 80% ethanol between tests.

Analyses

Each trial was recorded with a Logitech c920 HD Pro webcam placed 40 cm above the arena. In our analyses we accounted for spider species and age/sex category (adult male, adult female, subadult). From our footage we scored “initial heading,” defined as the final orientation toward any of the 4 goal platforms just before approach (either by walking or jumping toward it), suggesting initial

route preference (Tarsitano 2006). As the initial heading did not always coincide with the final chosen route, these data were qualified with “decided” if the initial heading coincided with the chosen route, or “undecided” if it changed. When spiders did not exhibit an initial heading, this was scored as N/A. We also scored the frequency of orientations during the scanning phase (i.e., a turn of the cephalothorax toward the goal platform while the spider was at the starting platform). The number of re-orientations during the detour were also recorded (see Supplementary Methods). Additionally, we measured “scanning duration” as the elapsed time from when the spider started scanning until it left the starting platform, as well as the time from the end of scanning phase to the end of the trial (“route duration”), the chosen route, the cardinal “direction” of the chosen route, and the position within the route at which the spider abandoned the route, or “giving up point” (Tarsitano and Jackson 1997). This was divided into 4 sections: (1) passing the magnetic base of the chosen route base but advancing no further; (2) climbing no more than half-way up the route; (3) reaching the second half of the route; and (4) reaching the goal platform or the last plastic articulation of the route (2.5 cm before the platform).

All analyses were done using R v.3.3.3 (R Development Core Team 2018). To determine route preferences, we performed 2 comparisons of multinomial probabilities for count data for each species. We calculated simultaneous confidence intervals (CIs) for the comparison of multiple odds between multiple multinomial samples (following Schaarschmidt et al. 2017) using the “multcomp” (Hothorn et al. 2008) and “nnet” (Venables and Ripley 2002) packages. We excluded highly influential data (outliers) from the model with a Cook's distance value (which combines the leverage and residuals of each data point) > 0.5 (Crawley 2007). The first analysis compared the probability of choosing a specific route (the route with the highest probability to be chosen) with the probability to choose the other 3 routes separately. Here, the baseline was the route with the highest probability of being chosen (short-lured route for *Trite*; long-lured for *Marpissa*). The second analysis compared the probabilities to choose either long or short routes, and either control or lured routes, plus their interactions (see Schaarschmidt et al. 2017).

To identify if spiders followed a specific route as a consequence of decision-making while on the starting platform and not by choices made after leaving the platform, we analyzed the final choice with respect to the initial heading for each species. Data from spiders that did not orient to any route before leaving the starting platform (N/A) were omitted. Here, we used a comparison of multinomial probabilities (for count data) to determine if the probability of a route being chosen depended on its congruence with the initial heading (i.e., “decided” spiders). Here we used 95% CIs, calculated using both Dirichlet (DP) and Wald methods. In these cases, a P value < 0.05 is found when “1” is contained within the CI for the odds ratio between decided and undecided spiders, such that the hypothesis that the groups are not different is rejected (Schaarschmidt et al. 2017).

Initial choice may not concur with the chosen route because spiders may not choose based on the last orientation toward a route before leaving the starting platform, but instead may survey the possible alternatives during the entire scanning phase. Consequently, the number of orientations during the scanning phase may be a better indicator of an association between the targeted route at the starting platform, and the chosen route at the end. In this case, we predicted that spiders that associate the correct route to their final goal (which we expected to be lured-routes, especially short ones)

would have a higher number of orientations during scanning. To determine this, we performed a GLM with a Poisson distribution with the number of orientations as the response variable. Spider category and chosen route were used as explanatory variables in the model for *Trite*, all of which completed routes. For *Marpissa*, we omitted 3 outliers (values: 14, 16, and 20 orientations). This model accounted for spider category, chosen route, and giving up point as explanatory variables, as several *Marpissa* did not complete routes. Contrast tests were then applied with the “gmodels” package (Warnes et al. 2015). Additionally, to determine whether the completion of the route (as a binary variable) depended on the number of goal orientations in *Marpissa*, we analyzed the data with a binary logistic regression, with completion of the route (0 = incomplete routes, 1 = completed routes) as the response variable and the number of goal orientations as the independent variable (Crawley 2007); we omitted one outlier for this analysis.

To investigate species-specific differences, we used the general dataset (this includes trials in which the individual chose a route irrespective of whether it was completed). Here, we performed a comparison of multinomial probabilities for count data, using the 4 routes as the categories (chosen route) and species as the treatment groups. The first analysis compared the baseline (short-lured) route with the other 3 routes. The second analysis was a specific comparison using the Wald and DP methods. The latter compared the probability to choose either control routes and lured routes, or short routes and long routes. To determine whether the number of orientations differed between species, we performed a GLM with a Poisson distribution, omitting N/A's and excluding outliers from 3 *Marpissa* individuals. Orientations were the response variable and species the explanatory variable. We used the same analysis, using data from completed routes only, to explore differences in the number of re-orientations (see Supplementary Methods).

We analyzed scanning duration and route duration using accelerated failure time regression (AFT) survival models, allowing us to compare the hazard function, or the risk of an event to finish, and a set of explanatory variables. Each AFT model was selected based on the distribution with the minimum AIC value, which exhibited the best fit to the data (Cox 1972). Second-order interactions among the explanatory variables were not accounted for, as the AIC value for the full model was higher than the selected model. Scanning duration was set as the response variable, with species, chosen route, and spider category as explanatory variables. With this configuration, we ran 2 AFT models using different datasets: the first model (Weibull distribution) used the general dataset, while the second used the subset of spiders that completed a route (“giving up point” = 4); in this model a log-logistic distribution was selected to better fit the data.

For route duration, the selected AFT model accounted for route duration as the response variable and species, spider category, and chosen route as the explanatory variables. Based on the AIC value, the best-fit error distribution for the general dataset was log-logistic. Additionally, we ran survival analyses using individuals that completed the route only; therefore, all 53 *Trite* individuals were included in the model, but only 25 *Marpissa*. Model selection was performed under the step model and here the best-fit error distribution was lognormal.

Results

For those spiders that made a choice, the log-odds between decided and undecided spiders did not differ between routes, either for *Trite*

or *Marpissa* (Figure 2, Table 1, and Supplementary Table S1 for probabilities). Additionally, when comparing control and lured-route choices, we found no difference in odds-ratio between decided and undecided *Trite* (95% CI for odds-ratio: DP method: lower = 0.35, upper = 12.01, Wald method: lower = 0.29, upper = 15.95) or *Marpissa* (95% CI for odds-ratio: DP method: 0.80, 15.16, Wald method: 0.75, 20.51), nor were there differences between long and short routes (*Trite*: DP method: 0.17, 5.47, Wald method: 0.13, 6.98; *Marpissa*: DP method: 0.10, 1.86, Wald method: 0.07, 1.99).

The number of orientations toward the chosen route was higher (estimate = 0.4908, $Z = 4.186$, $P < 0.0001$) in *Trite* (mean \pm SEM; 3.32 ± 0.45) than *Marpissa* (2.03 ± 0.32). *Trite* which chose the short-control route made significantly less orientations (Figure 3A) compared with the other 3 routes, and subadults oriented more than females and males (Figure 3B and Supplementary Table S2). In contrast, in *Marpissa*, the number of orientations was not influenced by chosen route or spider category, but was significantly higher among spiders that completed all 4 sections of the route, rather than those that gave up early (Figure 3C and Supplementary Table S3; note that no *Trite* gave up early). This was confirmed using a binary logistic regression which showed that *Marpissa*'s probability to complete routes was related to the number of goal orientations (95% CI = 0.029–0.509, Estimate = 0.2699, $Z = 2.203$, $P = 0.027$; Supplementary Figure S1). Similar trends were found with the number of re-orientations (Supplementary Figures S2, S3 and Supplementary Tables S4, S5).

In *Trite*, the probability to choose lured, compared with control, routes did not differ and there was no interaction between lure presence and route length (Table 2). Although the probability to choose the short-lured and short-control routes did not differ, *Trite* was more likely to choose short routes (Figure 4). In *Marpissa*, there were no differences in the probabilities to choose any route, nor were there any interactions, both among spiders that completed routes, and all spiders from the general dataset (Table 2). When comparing the general dataset for both species, the log-odds between choosing long-control with respect to short-lured routes and choosing long-lured compared with short-lured routes were significantly higher in *Marpissa* than *Trite* (Table 3). However, the odds ratio of choosing short-control with respect to short-lured routes did not differ between species (Figure 5). The odds ratio of choosing long routes with respect to short routes was significantly higher in *Marpissa* (95% CI for odds-ratio: DP method: lower = 2.05, upper = 15.98, Wald method: lower = 2.04, upper = 18.82). However, the odds ratio between control and lured routes did not differ between species (95% CI for odds-ratio: DP method: lower = 0.53, upper = 15.98, Wald method: lower = 0.51, upper = 4.70).

Across all spiders, the probability to remain at the starting platform scanning the surroundings (scanning duration) was not significantly affected by the chosen route (Supplementary Table S6). Nevertheless, there were species-specific behavioral differences, with *Marpissa* scanning for longer than *Trite* (max: *Trite* 966 s, *Marpissa* 1934 s; $P_1 = 0.016$; Figure 6A). Additionally, females scanned for longer than subadults (Figure 6B). The same effects were found when considering only individuals that completed a route (Figure 6C, D). The time to reach the giving up point was also unaffected by species, spider category, or by chosen route. However, route duration was lower in males than females, both for all spiders (Figure 7A and Supplementary Table S7) and among spiders that completed a route

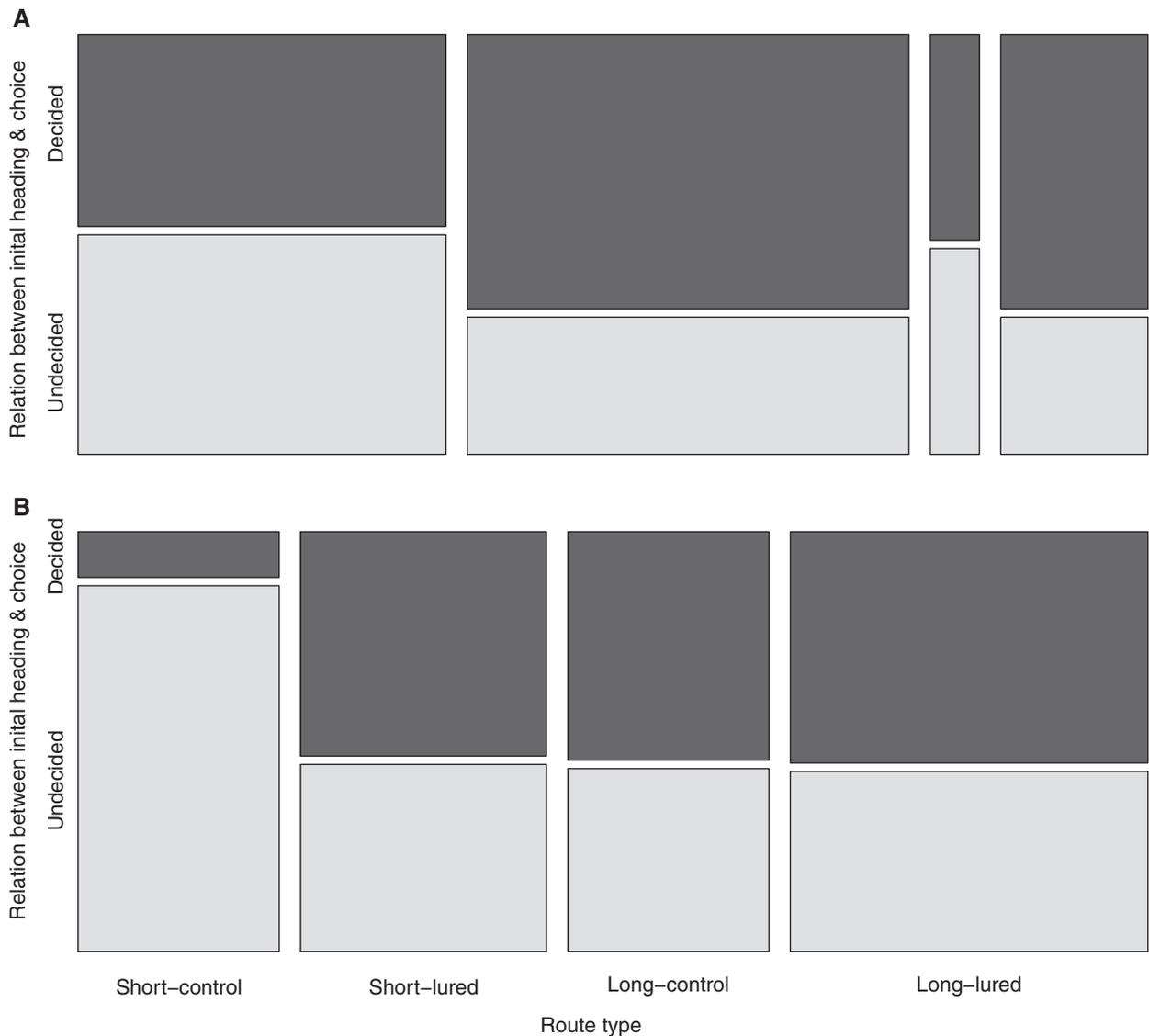


Figure 2. Mosaicplot showing the proportions of (A) *Trite* and (B) *Marpissa* spiders that did not change (decided) and those that changed their choice (undecided) for the 4 routes. Horizontal axis depicts the proportion of total spiders tested that used a given route type. Vertical axis depicts the proportion of total spiders tested that were decided or undecided for each given route type. The total area of each shaded section depicts the combined proportion of the given variables.

Table 1. Comparison of multinomial probabilities for number of decided/undecided spiders between the short control route and the other 3 routes chosen by *Trite* and *Marpissa*

<i>Trite</i>				
Comparisons between route variables (decided/undecided)	Estimate (odds-ratio)	SEM	Z	P
Short-lured/short-control	0.826	0.719	-1.149	0.561
Long-control/short-control	0.135	1.506	-0.089	1
Long-lured/short-control	0.826	1.008	-0.89	0.783
<i>Marpissa</i>				
Short-lured/short-control	2.262	1.221	-1.852	0.129
Long-control/short-control	1.856	1.255	-1.479	0.26
Long-lured/short-control	2.33	1.174	-1.985	0.097

(Figure 7B). In the latter subset, *Trite* was faster than *Marpissa*, (Figure 7C) and spiders that chose long routes took longer than those choosing short routes (Figure 7D and Supplementary Table S8).

Discussion

This study provides evidence of cognitive limitations while performing spatial tasks in 2 salticid species, contributing to a broader view of the differences of spatial ability within the Salticidae. In

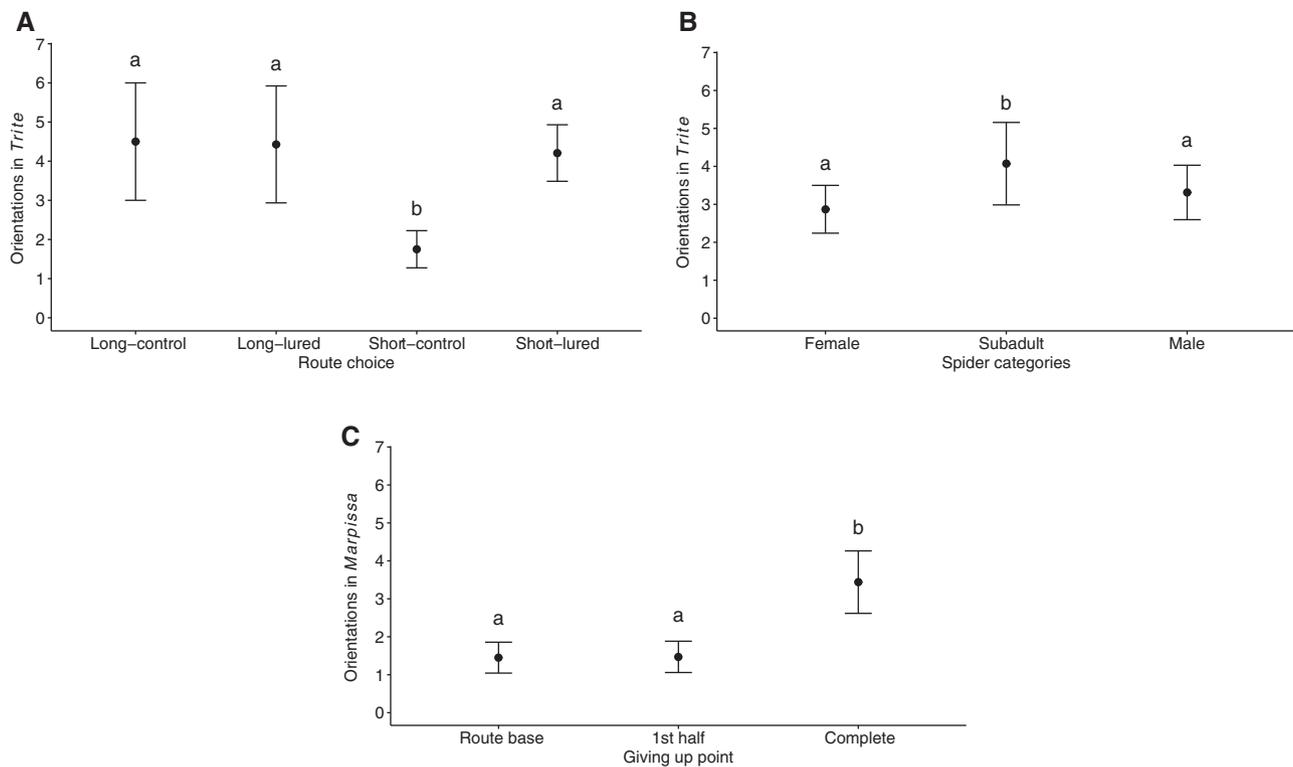


Figure 3. Mean (\pm SEM) number of orientations by (A) chosen route in *Trite*, (B) *Trite* spider category, and (C) giving up point in *Marpissa*. Letters indicate significant differences between groups.

comparison with previous studies, our detouring tasks were especially complex (4 choices varying in length and presence of prey and in which visual access to prey was denied after leaving the starting platform). Nevertheless, we found evidence that spiders are able to make decisions while on the starting platform before embarking on a route, and we also observed interspecific differences in route-choice behavior. While we anticipated that the short-lured route would be preferred, due to being more efficient (shorter) and containing prey, spiders did not exhibit this preference. *Trite* did prefer short over long routes, but showed no preference for lured routes, possibly because the task was too cognitively demanding. In *Marpissa*, spiders showed no route preference, and may have chosen routes randomly. However, arguing against this, in their frequency of orientations and re-orientations, *Marpissa* demonstrated some evidence that they can discriminate lured from control routes.

Route choice did not affect scanning or route duration for either species, but *Trite* completed routes faster than *Marpissa*, which may have struggled more to solve the task than *Trite*: although *Marpissa* spent more time scanning, the number of orientations was lower than *Trite*'s, and *Marpissa* only completed routes when they frequently oriented (and re-oriented) toward the goal platform. Indeed, compared with the salticid *Portia*, *Trite*'s fast performance in spatial tasks previously suggested to us that *Trite* faces a trade-off between fast route completion but deficient route assessment (Aguilar-Arguello et al. 2019). We cannot discard that previous experience with houseflies in nature may have caused different behaviors between species, as we have little information about housefly availability in their natural habitats, other than they exist in both habitats. However, for decades houseflies have been used as standard prey for predator-related experiments for both of these species (e.g., Forster 1977, 1979; Tarsitano and Jackson 1992; Jackson and Tarsitano

1993), confirming that houseflies are attractive prey. We also found that spider categories behaved similarly across species, with subadults finishing the scanning phase faster. As it is known that adults are more capable at solving learning tasks than juveniles (Edwards and Jackson 1994; Skow and Jakob 2005; Hill 2006), this suggests that they may require experience to develop attentional skills for spatial tasks. Spiders are strongly influenced by innate behavior; however, cognitive skills are flexible enough for innate behaviors to be perfected (Forster 1977; Edwards and Jackson 1994; Bartos and Szczepko 2012). Thus, it is reasonable to expect better performance in adults than in subadults, but, unfortunately, few performance differences were observed. Nevertheless, males completed routes faster than subadults and females. The speed at which males completed routes was surprising, as previous work indicates that females are more motivated than males in predation-based (Jackson and Wilcox 1990) or learning (reviewed in Jakob and Long 2016) tasks. Because of this, few studies of this type have included males, yet previous work (Aguilar-Arguello et al. 2019) and this study suggests that males may be more mobile than females, possibly because they actively search for mates at this life stage (Jackson and Pollard 1997), and this is something that should be considered in future work. We observed that males were more active than females and subadults, especially among *Trite* individuals, in which males tended to be more skittish (personal observation).

If salticids are motivated and capable of choosing and completing difficult detours in which visual contact with the goal is lost, we believe they will exhibit 3 key components. These are the initial heading (to some extent, as discussed below), their final choice coinciding with the initial heading, and the fact that they re-orient toward the goal during the detour. However, this combination appears to be cognitively challenging: only 3 *Marpissa* and 12 *Trite*

performed all 3, while 87% ($n = 101$) of 116 spiders tested lacked at least one of these 3 components in their detour.

Although we predicted that spiders would be able to discriminate lures and associate their location with the goal platform while still on the starting platform, the proportion of decided spiders did not differ from that of undecided individuals in either species, nor was this affected by route. This suggests that either: (1) the initial heading is not a good indicator of decision-making regarding chosen route, or (2) that the initial heading indicates a decision, but is often unclear because spiders are not motivated enough to follow the entire route.

In relation to the first hypothesis, that initial heading is a poor indicator of decision-making regarding the chosen route, Tarsitano

and Jackson (1994) observed that, while scanning, *Trite* (and *Portia*) first focuses on the goal and then fixates on the different components of the detour, making it difficult to determine a variable that depicts the chosen route during the scanning stage. Thus,

Table 2. Results from comparisons of the probability to choose the short-lured route in *Trite* and *Marpissa* spiders with the other 3 routes, and comparisons between probabilities of choosing routes by length and/or presence of lure

	Log-odds	SEM	Z	P
<i>Trite</i> *				
Comparisons between routes				
Long-lured/short-lured	-1.232	0.429	-2.868	0.012
Long-control/short-lured	-2.489	0.736	-3.376	0.002
Short-control/short-lured	-0.182	0.302	-0.602	0.901
Comparisons between route variables				
Control-routes/lured-routes	-0.717	0.428	-1.674	0.210
Short-routes/long-routes	1.767	0.428	4.124	0.0001
Interaction ^a	-0.535	0.428	-1.249	0.429
General dataset (<i>Marpissa</i>)**				
Comparisons between routes				
Long-control/long-lured	-0.559	0.361	-1.546	0.297
Short-lured/long-lured	-0.336	0.338	-0.995	0.649
Short-control/long-lured	-0.336	0.338	-0.995	0.649
Comparisons between route variables				
Control routes/lured routes	-0.279	0.257	-1.089	0.618
Short routes/long routes	-0.056	0.257	-0.22	0.995
Interaction ^a	-0.279	0.257	-1.089	0.618
Dataset for completed routes (<i>Marpissa</i>)***				
Comparisons between routes				
Long-control/long-lured	-0.559	0.626	-0.893	0.71
Short-lured/long-lured	-5.13e-06	0.534	0	1
Short-control/long-lured	-5.13e-06	0.534	0	1
Comparisons between route variables				
Control routes/lured routes	-9.225	47.510	-0.194	0.860
Short routes/long routes	-8.127	47.510	-0.171	0.878
Interaction ^a	-8.820	47.508	-0.186	0.867

Marpissa: data from all individuals that chose a route (general dataset) and from completed routes dataset. *P* values by route: *Long-lured ($n = 7$, $P = 0.132$), long-control ($n = 2$, $P = 0.037$), short-lured ($n = 24$, $P = 0.452$), short-control ($n = 20$, $P = 0.377$)., **Long-lured ($n = 21$, $P = 0.333$), long-control ($n = 12$, $P = 0.190$), short-lured ($n = 15$, $P = 0.238$), short-control ($n = 15$, $P = 0.238$)., ***Long-lured ($n = 7$, $P = 0.28$), long-control ($n = 4$, $P = 0.16$), short-lured ($n = 7$, $P = 0.28$), short-control ($n = 7$, $P = 0.28$).
^a Model accounts for the interaction between route length and lure incidence.

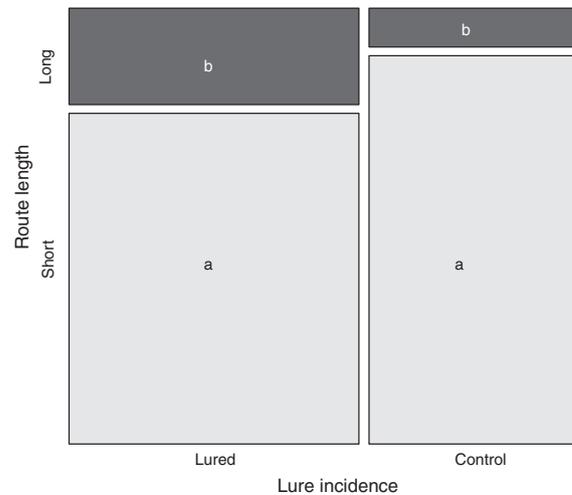


Figure 4. Mosaicplot of the frequency of choices for the 4 different routes in *Trite planiceps*. Horizontal axis depicts the proportion of total *Trite* tested that went toward lured or control routes. Vertical axis depicts the proportion of *Trite* that used long or short routes. The total area of each shaded section depicts the combined proportion of the given variables. Letters denote significant differences.

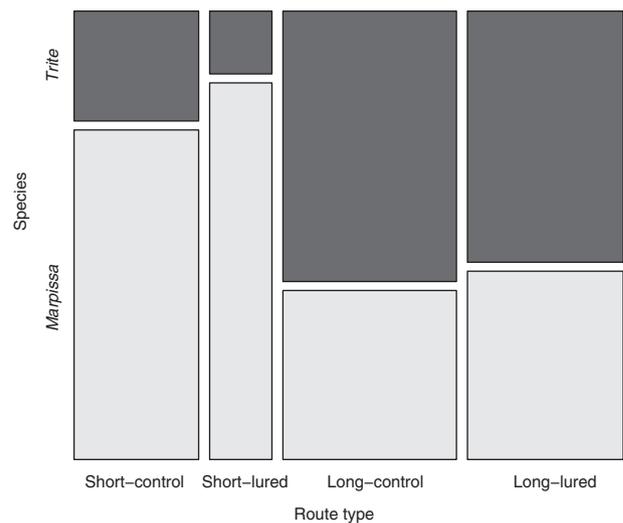


Figure 5. Mosaicplot of proportion of choices for each route in both spider species. Horizontal axis depicts the proportion of total spiders tested that used a given route type. Vertical axis depicts the proportion of each species that used a given route type. The total area of each shaded section depicts the combined proportion of the given variables.

Table 3. Results from the multinomial comparison of the number of individuals of each spider species that chose each route

Comparisons between routes (<i>Marpissa/Trite</i>)	Log-odds	SEM	Z	P
Long control/short-lured	-2.261	0.837	-2.720	0.019
Long-lured/short-lured	-1.568	0.546	-2.870	0.012
Short control/short-lured	-0.182	0.474	-0.384	0.969

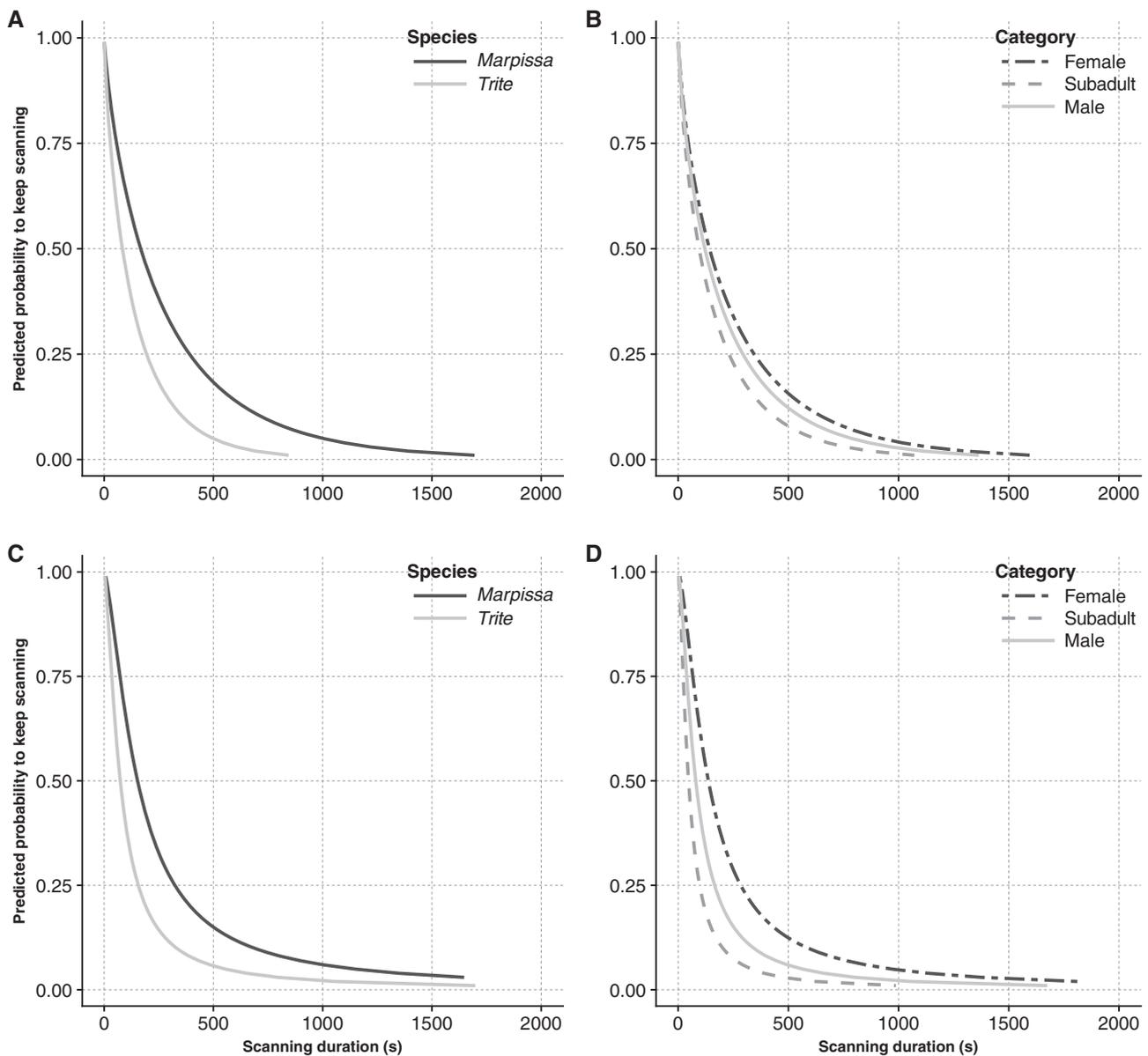


Figure 6. Accelerated failure time model curves depicting the probability of continuing scanning over time for (A) all *Marpissa* and *Trite*, irrespective of whether routes were completed, illustrating that *Marpissa* scanned for longer than *Trite* (B) combined spider categories of both species, irrespective of whether routes were completed, depicting that the female category scanned the longest (C) data from spiders that completed routes for *Marpissa** and *Trite***, (D) spider categories from spiders that completed routes***. Values of routes with duration >2000 s not shown: * $n=2$; ** $n=1$; *** $n=1$.

decision-making may instead result from the information compiled during the entire scanning process, rather than relying on the last orientation in the scanning routine. If the initial heading is a poor indicator of decision-making, the number of orientations toward a given route may be more indicative of route choice. Our data support the idea that the number of orientations toward a goal during scanning may be a better indicator of choice than initial heading, although how this works is presently unclear. In *Marpissa*, route completion was higher among spiders that performed a high number of orientations, while in *Trite* both the number of orientations and re-orientations were lower for routes that were more frequently chosen.

Evidence for the second hypothesis, that the initial heading is a good decision indicator, is provided by Tarsitano's (2006) work, where *Portia* went to the platform on the same side as their

initial heading ("decided") significantly more often than those "undecided" spiders that changed sides from their initial heading (19 versus 7; $\chi^2 = 5.538$, $P=0.019$; Chi-square test of independence). Our experiment provided limited support for this hypothesis: for both species, but especially among *Trite*, the ratio of decided/undecided spiders did not differ, suggesting that initial heading alone is not always a good predictor of chosen outcome.

Inability to discriminate the presence or absence of prey seems unlikely as an explanation for our observed lack of route preferences. Goal platforms were 17 cm away from the starting platform and salticid vision is accurate within 30 cm (Jackson and Blest 1982). We also doubt that detour length was too challenging, as similar detour lengths have been tested, even with a hidden lure after leaving the starting platform (Tarsitano and Jackson 1997 = 139 cm; Cross and Jackson 2016 = 77.5 cm). However, previous successful

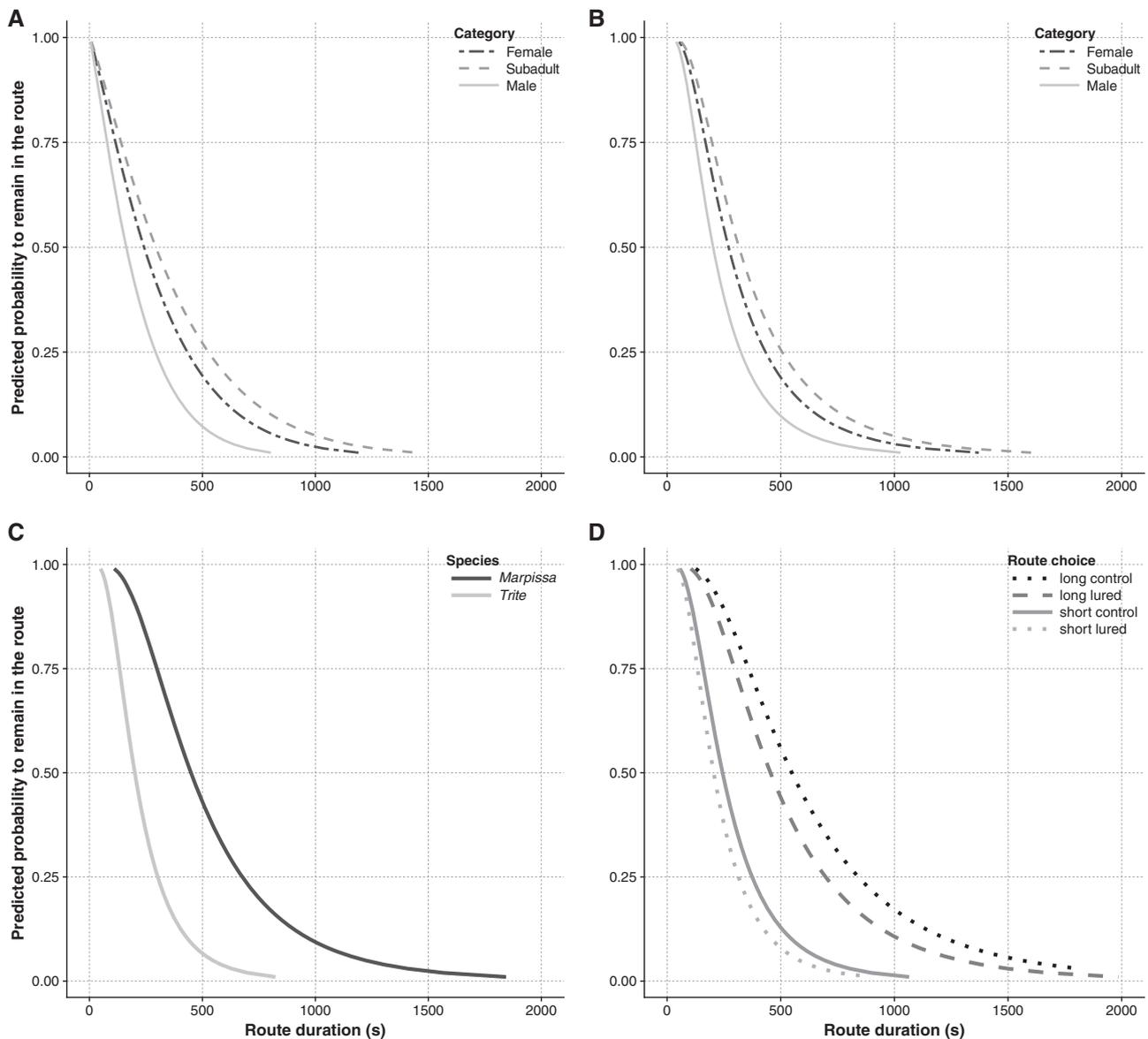


Figure 7. Accelerated failure time model curves depicting the probability of continuing on the chosen route over time for each spider category spiders for (A) all spiders, irrespective of whether routes were completed, depicting that route duration was lower in males than females and (B) spiders that completed routes only, also depicting that route duration was lower in males than females. (C) Species differences between *Marpissa* and *Trite* that completed routes, depicting that *Marpissa* spent longer *en route* than *Trite* and (D) route category for spiders that completed routes (data not shown for 2 individuals choosing long-control route, as these lasted >2000 s), depicting that spiders choosing long routes took longer than those choosing short routes.

experiments have been on *Portia* and other Spartaeinae genera, which have exceptional cognitive ability among salticids (Jackson and Pollard 1996; Jackson and Cross 2011), and despite this, the execution of long detours with a hidden lure is difficult for *Portia* (Tarsitano and Jackson 1997). Non-spartaeines, including *Trite* and *Marpissa*, have performed well in detours up to 35 cm (Tarsitano and Jackson 1992), and *Trite* has completed 125 cm-long detours when a moving lure was visible throughout (Tarsitano and Jackson 1994). Possibly what made the present experiment especially difficult was that the lure was visible only from the starting platform, so spiders had to remember the goal's location.

Detouring requires the association of secondary objectives with the primary objective and the use of spatial memory to remember the exact location of the goal (Hill 1979), but visual input may require constantly updating (i.e., re-orientations) to keep motivated

and maintain associations. Our data suggest that performing re-orientations is a strong indicator of motivation: *Marpissa* individuals that completed routes (34%) re-oriented to the goal platform more often than those that did not (Supplementary Figure S3). In the case of complex detours, once visual contact with the goal is lost, the association between secondary and primary objectives may be severed, such that the spider cannot keep track of the detour. However, *Portia* and a few Spartaeinae species can follow long and intricate detours without the need to constantly update the primary goal's location (Jackson and Wilcox 1993) and without experience (Tarsitano and Jackson 1997; Cross and Jackson 2016). In contrast, non-spartaeines (including *Trite* and *Marpissa*) can only solve spatial tasks with visual access to a moving prey or when they have had previous experience (Nakamura and Yamashita 2000; Skow and Jakob 2005; Hill 2006; VanderSal and Hebets 2007; Liedtke

and Schneider 2014). Coupling results from those previous studies and ours, we suggest that the species used here can also perform detours as complex as those made by *Portia*, but may require experience to achieve this demanding spatial task. What is surprising in *Portia* is its ability to plan ahead of time, and its ability to associate visual cues without previous experience. This could be unique not only among salticids, but among invertebrates.

Variation in spatial performance across salticid species is known. For example, despite its ability to complete different types of simple detours (Hill 1979), *Phidippus audax* failed in detours that required initially moving away from the goal for the correct detour (reverse-route detours; Carducci and Jakob 2000), which can be solved by *Trite* (Tarsitano and Jackson 1994). This variation in spatial ability has been attributed to the environmental structure in which each species lives (Tarsitano and Andrew 1999), with complex habitats presenting a more cognitively challenging navigational milieu (Gauin and FitzGerald 1986; Costanzo et al. 2009; Schwarz and Cheng 2010; Clarin et al. 2013; Schultheiss et al. 2016). The relationship between habitat attributes with performance in our study species fits this model, although significantly more comparative work in this area is needed. For instance, *Marpissa*'s struggle to complete the route may be a consequence of the lack of vertical routes in their natural environment, which primarily consists of small rounded rocks and a few pieces of driftwood. All *Trite* completed the routes and performed faster than *Marpissa*, which may be facilitated by adaptations to navigate within the vertical flax leaves that characterize its habitat.

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Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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