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How jumping spiders (Araneae: Salticidae) find and use indirect routes to reach their sighted objectives

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Abstract. Jumping spiders (Salticidae) are not limited to planning their route at the onset of pursuit, but dynamically collect and use new information as they complete an indirect route or detour. There is strong support for the hypothesis that selection of the immediate route is based on the presence of a visible connection leading to the objective. In turn salticids can use these visible connections as secondary (or intermediate) objectives. Salticids can compute the expected direction and distance of their primary objective after they move to a new location, and frequently turn (*reorient*) to face their original objective to begin a new segment of pursuit. Completion of a sequence of these pursuit segments allows the salticid to successfully complete a complicated and indirect route of pursuit even when this is not visible at the onset.

Key words. *Anasaitis,* cognition, *Colonus,* detour, direction information, distance information, gravity information, *Habronattus, Hentzia,* landmarks, *Lyssomanes, Maevia,* map direction, orientation, *Phidippus, Platycryptus, Portia,* reorientation, route selection, secondary objectives, segmented pursuit, Spartaeinae, spatial integration, visual cues

The ability of salticid spiders to complete detoured or indirect pursuits of visual objectives has been known for some time (e.g., Bilsing 1920; Heil 1936; Hill 1977, 2008, 2018a; Jackson & Wilcox 1993). The idea that a number of spartaeine spiders including *Portia* plan their route at the onset of pursuit has been suggested in a series of publications (e.g., Tarsitano & Jackson 1997; Tarsitano & Andrew 1999; Cross & Jackson 2016). However later observations led Tarsitano (2006) to conclude that these spiders use information collected during their movement to identify routes, and that they also pursue intermediate objectives en route to their prey. This agrees with my earlier studies on the dynamic use of distance and direction information by salticids during their pursuit of sighted objectives (Hill 1978, 1979, 2007, 2010).

It is my assessment that the mathematics associated with my earlier studies (expanded in Hill 2010), primarily related to the use of information related to direction and distance by these spiders, made this work less accessible to a wider community that includes many serious students of arachnid behavior. Here I will present a more limited qualitative description of the route selection behavior that makes these complicated detours possible, using a series of drawings of hypothetical pursuits. I will also avoid the use of terms like *cognition* and *orientation* that have limited utility because of their multiple and imprecise definitions. The symbolic depiction of salticid positions and movement described previously (Hill 2010; see Figure 2) is used here.

Although related abilities can vary, in general salticid spiders remember the relative position of their prey as they pursue it, and they can turn to face that position after moving to a new location (*reorientation*, Figure 1). This ability, prerequisite for the completion of a complex detour, is based on their ability to assess the distance and direction of their prey as well as the distance and direction of their own movement. For details related to the integrated use of idiothetic (*self-motion*) information, landmarks, route-reference (combined use of idiothetic and/or landmark information) and gravity by salticids you should read my earlier analysis (Hill 2010).



Figure 1. Composite of four photographs showing sequential (1-4) positions assumed by an adult male *Phidippus princeps pulcherrimus* Keyserling 1885 during the pursuit of a sighted fly. For more information on the biology of this spider see Hill (2018b). Relative positions are expressed as vectors in this diagram. In effect this jumping spider computed the relative position of its prey from a new location (\overline{D}_{CA}) by subtracting its combined movement vector (\overline{S}) from the original relative position of its prey (\overline{D}). The resultant turn (at position 4) is called *reorientation* with respect to the primary objective of the pursuit. See Hill (2010) for details related to the integration of distance and direction information by these spiders. A symbolic depiction of this pursuit sequence is shown in Figure 2.



Figure 2. Symbolic description of pursuit shown in Figure 1. In this and in subsequent diagrams the primary objective (A) is represented by a black circle, secondary or intermediate objectives by grey circles (B, C, D), and positions assumed by the spider by white circles (S). Vectors representing either the original orientation to the prey position (1) or subsequent reorientation to that position (3) are highlighted in red. Movement by the spider (2) is indicated as a dashed line. Not shown here, vectors representing turns to face secondary objectives or plant positions are shown in black. Here the spider faced its prey (1), turned and ran (2) up to a higher position with a closer map (horizontal) distance to that prey, and then *reoriented* to face the expected position of that prey (3).

Here I will present a series of diagrams (Figures 3-11) to show how a salticid *could* use this memory of relative position to dynamically solve a problem of indirect access. When the route of approach to an objective lies in a single plane (Figures 3-4), salticids consistently move in the direction of a visibly connected path leading from the position of the spider to the prey position. Unless this route leads directly to that prey, the spider will need to turn away to follow this route.



Figure 3. Hypothetical pursuit of sighted prey (A, *primary objective*) in a plane. This assumes that the position of the prey is too far away for a direct jump. **1**, Spider (S) facing the prey (A). **2**, Spider facing a secondary objective (B), selected for its visible connection to the primary objective (A). **3**, Spider moving along in the direction of (B). **4**, Spider facing the expected position of its prey from a new position (*reorientation*), initiating a second segment of pursuit. **5**, Spider moving to the secondary objective (B) on the second segment of pursuit. **6**, Spider facing the expected position of its prey from this new position (reorientation), initiating a third segment of pursuit. **7**, Spider moving toward the prey position. At all times during this pursuit the route would be visibly connected to the prey position.



Figure 4. Hypothetical pursuit of nearby prey (*primary objective*) in a plane. **1**, Spider facing the prey. **2**, Spider facing a secondary objective (B) selected for its visible connection to the primary objective (A). **3**, Spider facing a tertiary objective (C) selected for its visible connection to the secondary objective (B). **4**, Spider moving away from the prey position toward the tertiary objective. **5**, Spider reorienting to face the original prey position. **6**, Spider moving toward the prey on the second segment of pursuit. **7**, Spider reorienting to face the original prey position. **8**, Spider moving toward its prey on the third segment of pursuit. As in the simpler example shown in Figure 3, the route would be visibly connected to the prey at all times during this pursuit.

When an entire route connecting the spider to its primary objective does not lie in a plane, observation of a connection leading to that prey may be more difficult. Examples shown here (Figures 5-7) compare in complexity with route problems solved by a series of spartaeine salticids (Cross & Jackson 2016). It is quite possible that some salticids are not as capable of recognizing or using these connections in certain contexts. In the first example (Figure 5) the continuity of the entire route, although twisting, would be visible during the entire pursuit, and in fact all positions on that route are *almost* coplanar in a vertical plane. For many *Phidippus* and *Portia* problems like this are not difficult.



Figure 5. Hypothetical pursuit of nearby prey (*primary objective*) in three dimensions. In this example the entire route is almost coplanar and would be visible to the spider at all times during its pursuit. **1**, Spider facing the prey (A). **2**, Spider facing a secondary objective (B) selected for its visible connection to the primary objective (A). **3**, Spider moving down (the only option available at this point) to complete segment one of pursuit. **4**, Spider reorienting to face the primary objective (A) to begin the second segment of pursuit. **5**, Spider facing the secondary objective (B). **6**, Spider facing a tertiary objective (C) connected to the secondary objective (B). **7**, Spider moving to the tertiary objective. **8**, Spider reorienting to face the primary objective, initiating a third segment of pursuit. **9**, Spider moving toward the primary objective.

A more complicated version of the same problem (Figure 6) would require the spider to turn away from its secondary objective. Although points along this route are definitely not coplanar, the entire route shown here is still visibly connected at all positions during pursuit. The ability of the spider to reorient to the primary objective should greatly facilitate route selection in this case, and the relationship of the route to the primary objective becomes more linear and presumably easier to detect in each successive segment of pursuit. Each successive reorientation can present the spider with a new and simpler access problem to solve. For example, at the onset of the third segment in this pursuit (9, reorientation) the remaining connection is coplanar. At the onset of the fourth segment (11, reorientation) the route of approach is directly ahead and unambiguous.



Figure 6. Hypothetical pursuit of nearby prey (*primary objective*) in three dimensions with a route that was not coplanar. In this example the entire route would be visible to the spider at all times during the pursuit. **1**, Spider facing the prey (A). **2**, Spider facing a secondary objective (B) selected for its visible connection to the primary objective (A). **3**, Spider moving down (the only option available) to complete segment one of this pursuit. **4**, Spider reorienting to face the primary objective (A), to begin the second segment of pursuit. **5**, Spider facing the secondary objective (B). **6**, Spider facing a tertiary objective (C) selected for its visible connection to the secondary objective (B). **7**, Spider facing a quaternary objective (D) selected for its visible connection to the tertiary objective (B). **8**, Spider moving to the quaternary objective (D). Movement toward the quaternary objective rather than toward the tertiary objective would indicate that the spider recognized that the elevated position of the latter was not directly accessible. **9**, Spider reorienting to face the primary objective (A) to begin a third segment of pursuit. **10**, Spider moving toward the primary and secondary objectives. **11**, Spider reorienting to face the primary objective (A).

In some cases the route of access may not be visible for its entire length at the onset and the spider may be much more dependent on its ability to reorient from a new position to find a complete route. One example of this can be seen in the problem shown in Figure 7, very similar to real problems successfully solved by many spartaeines in the laboratory (Cross & Jackson 2016). In this example the spider (facing D at 7) could not see that its first quaternary connection (D) was not connected to its tertiary connection (C), but corrected for this from a subsequent position (facing D' at 11) where the relationship of a second quaternary connection (D') became visible. Successful completion of these detours with a *hidden path* provides strong support for the hypothesis that the spider's continuous memory of the relative position of the primary objective is a prerequisite for the negotiation of a complex route of access, allowing a discovered route to be completed dynamically as a series of visible segments. Although a series of reorientations are shown here, these are not always required for some salticids (*Phidippus*, Hill 2010; Figure 1) to maintain their memory of the relative position of a primary objective as they move.



Figure 7. Hypothetical pursuit of nearby prey (*primary objective*) in three dimensions with a non-coplanar route that was not always visible to the spider. **1**, Spider facing the prey (A). **2**, Spider facing a secondary objective (B) selected for its visible connection to the primary objective (A). **3**, Spider moving down (the only option available) to complete segment one of this pursuit. **4**, Spider reorienting to face the primary objective (A) to begin a second segment of pursuit. **5**, Spider facing the secondary objective (B). **6**, Spider facing a tertiary objective (C) selected for its visible connection to the secondary objective (C). **8**, Spider moving to the quaternary objective (D). **9**, Spider reorienting to face the primary objective (A) beginning a third segment of pursuit. **10**, Spider turning to face the tertiary objective (C). **11**, Spider turning to face a new quaternary objective (D'), now visibly connected to the tertiary objective. **12**, Spider moving to the quaternary objective. **13**, Spider moving to face the primary objective. **15**, Spider moving toward the secondary and tertiary objectives. **16**, Spider reorienting to face the primary objective. **17**, Spider moving toward the secondary and tertiary objectives. **18**, Spider reorienting to face the primary objective (A), beginning a fifth segment of pursuit. **19**, Spider moving directly toward the primary objective.

The ability of these spiders to find and to use a *hidden path* (a portion of the access route not visible at the onset of a pursuit) can clearly be critical to their success. This is represented here by three additional hypothetical problems associated with planar pursuit (Figures 8-10). In the first two problems (Figures 8-9) the spider initially would not see a break in its access to the primary objective along what would appear to represent the most direct route of access. In each case continued execution of a program of segmented or dynamic pursuit would still result in successful access to that objective, even when the resultant route was longer than necessary.



Figure 8. Hypothetical pursuit of nearby prey (*primary objective*) using a coplanar route with a break that was not visible to the spider at the onset (1). **1**, Spider facing the prey (A). **2**, Spider moving toward the prey (A). **3**, Spider reorienting to face the prey, initiating a second segment of pursuit. At this point the spider determined that the prey was too far for a direct jump. **4**, Spider turning to face a secondary objective (B), selected for its visible connection to the primary objective (A). **5**, Spider moving toward the secondary objective (B). **6**, Spider reorienting to face its prey (A), initiating a third segment of pursuit. **7**, Spider facing its secondary objective (B). **8**, Spider moving toward its secondary objective. **9**, Spider reorienting to face its prey (A), initiating a fourth segment of pursuit. **10**, Spider moving toward its secondary objective (B). **11**, Spider reorienting to face its prey (A), initiating a fifth segment of pursuit. **12**, Spider moving toward its prey.



Figure 9. Hypothetical pursuit on a coplanar route with multiple connections that must be discovered during the pursuit. Symbology depicting turns and movement through a series of positions (1-14) follows that used in previous examples. As shown in the pursuit depicted in Figure 8, a spider behaving as shown here would not follow the shortest possible route to reach its objective (A), but it would not lose track of the relative position of that objective. This would allow it to discover each *hidden path* required to successfully complete the pursuit.

In the previous examples, a spider could make progress just by continuing to follow its program. But what happens if a spider runs into a dead-end on its route? Figure 10 depicts a situation in which a spider (at position 3) discovers a break in its route that can be dealt with by continuing the program, but then reaches an unexpected dead end (at position 6). From this new position(6), however, the entire connected route would be visible to the spider, and it could then initiate a new pursuit in the opposite direction (Figure 11) without any difficulty.



Figure 10. Hypothetical pursuit on a coplanar route that leads to an unexpected break and then to a dead-end. When the spider initially (position 1) faces the objective it cannot see the discontinuity at positions 3 and 6. The gap at position 3 could be addressed through pursuit of a secondary objective, but this leads to a second break in the path (visible at position 6) and a dead end [?].



Figure 11. Solution for dead-end encountered in Figure 10. From position 6 the complete route, without any breaks, would be visible to the spider. By restarting its pursuit in the opposite direction the problem of access could be resolved by a salticid by simply following that connected pathway in a clockwise direction.

Many more problems of this kind can be devised and tested in the laboratory to determine the capabilities and limitations of different salticid species. However to really understand this behavior we need to return to the field to observe the effect of microhabitat on the geometry of pursuit (Figure 12).



Figure 12 (continued on next page). Representative salticids and their microhabitats in southern Greenville County, South Carolina. **1-2,** Female *Lyssomanes viridis* (Walckenaer 1837) with brachyceran fly, and the evergreen tree *Magnolia grandiflora*. *L. viridis* live on or beneath large leaves in the forest understory. **3-4,** Female *Colonus sylvanus* (Hentz 1846) feeding on spider, and the small evergreen tree or shrub *Prunus caroliniana*. This is a common predator on spiders and insects in the forest understory. **5-6,** Female *Platycryptus undatus* (De Geer 1778) with nematoceran prey, and trunk of the Virginia Pine, *Pinus virginiana*. *P. undatus* are dorsoventrally compressed and make their shelters under loose bark, often on dead or dying trees, or in crevices on the outside of man-made structures.



Figure 12 (continued from previous page, continued on next page). Representative salticids and their microhabitats in southern Greenville County, South Carolina. **7-8**, Female *Maevia inclemens* (Walckenaer 1837) with brachyceran fly, and leaves of the Virginia Creeper *Parthenocissus quinquefolia* in the forest understory. *Maevia* are leaf-dwellers, very adept at flipping from one side of a leaf to the other. **9-10**, Female *Phidippus princeps* (Peckham & Peckham 1883) feeding on spider, and dense growth of herbs and grasses including Solidago along a forest margin. **11-12**, Male *Phidippus pius* Scheffer 1905 feeding on cicadellid leafhopper *Graphocephala coccinea*, and tall grasses with herbacious plants in a well-developed old field.



Figure 12 (continued from previous page). Representative salticids and their microhabitats in southern Greenville County, South Carolina. **13-14**, Female *Hentzia mitrata* (Hentz 1846) feeding on large brachyceran fly, and leaves of of a deciduous shrub or small tree of the genus *Prunus* in the woodland understory. **15-16**, Female *Anasaitis canosa* (Walckenaer 1837) feeding on ant worker, and the fallen branches and leaf litter of its habitat in the woodland understory. **17-18**, Male *Habronattus coecatus* (Hentz 1846) feeding on captured mosquito (Culicidae), and its open-ground habitat.

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Clearly the microhabitat, prey, and predatory tactics in use by salticid spiders can vary greatly. For example, I have only seen *Platycryptus undatus* jumping to capture flies after a direct approach on a relatively flat surface, usually in the morning when these flies are still cool and slow. *Maevia inclemens* are adept at moving between leaf surfaces and can leap quickly in any direction to capture a flying insect as soon as it lands nearby. *Phidippus* species in an open field often face downward on a plant stem waiting for active or fast-moving prey to appear, and they are generally adept at finding their way through an array of stems and leaves. They may also deploy a number of different tactics based on the prey that are available, and will stalk and feed on other spiders. Detours may not be so important to hopping ground-dwellers like *Habronattus coecatus*, although I have watched one male make a carefully concealed approach to a potentially dangerous female. The ground-dwelling *Anasaitis canosa* have great skill related to the tracking and capture of moving ants that may include an ability to predict their movement in a manner that allows them to be intercepted (Hill 2006). We still know little about the recognition and evaluation of common objects (e.g., leaves, stems and branches) encountered and utilized by salticids.

As noted previously the detouring prowess of spartaeine salticids that feed on other spiders has received much attention in recent years. It has been suggested that predation on spiders (*araneophagy*) correlates positively with detouring capability (Jackson & Cross 2011; Cross & Jackson 2016). Salticids of the genus *Colonus* frequently, but not exclusively, detect and pursue immobile prey that includes resting spiders. Each of their pursuits can be exceedingly slow, often taking many minutes to complete (Hill 2018a). They are quite capable of completing detours in the course of pursuit, but there is no reason to believe that their detouring ability is greater than that demonstrated by generalists of the genus Phidippus (Hill 2010). However there is certainly much more time available to pursue immobile or slowly-moving prey, and risk/reward economics should play a role in the evolution of related behavior including persistence in completion of an approach. At the same time lack of persistence should not be interpreted as a sign of low intelligence. For many salticids route selection can also include decisions related to concealment from wary prey, including the possibility of approach on the opposite side of a stem or leaf (Hill 2010, 2018a). Tactics can also vary greatly with respect to the type of prey or the age of the pursuing spider (Edwards & Jackson 1993, 1994; Bartos & Szczepko 2012). We have much to learn about the predatory versatility of salticid spiders, and many discoveries await the patient observer of their behavior in a natural setting.

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