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Predatory pursuit of ants by *Anasaitis canosa* (Araneae, Salticidae)

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1. Preface

This report is the result of several relatively recent observations of the jumping spider *Anasaitis canosa* dating from late 2005. These observations were made possible by the current affordability of digital motion pictures, something that did not exist in the 1970's when I began my study of salticid behavior, on a very limited budget. This report also provides a platform for clarification of hypotheses related to selection of routes of pursuit or other kinds of movement by various salticid spiders, with reference to some of the more recent literature pertaining to the subject.

2. Summary

Predatory pursuits of rapidly running ants by ant-eating jumping spiders (*Anasaitis canosa*) were observed and filmed in their natural leaf-litter habitat in upstate (Greenville County) South Carolina. The general features of indirect or detoured pursuit of prey by salticid spiders, including movement along routes of rapid access, and reorientation toward the expected position of prey from new positions along the route of pursuit, were observed. The ability of these spiders to approach rapidly moving ants that were frequently concealed in the leaf litter, and to move to positions where these ants could then be captured when they reappeared, was demonstrated.

This can be viewed as *intelligent* behavior, to the extent that we can agree that intelligence is demonstrated by the processing and meaningful use of large amounts of information by an animal. The language used to describe salticid behavior can be misleading, and we presently do not have the tools required to assess the actual experience, perception, or conceptual frameworks associated with the behavior of these spiders.

The general ability of salticid spiders to move toward *secondary objectives* (or positions that facilitate access to a *primary objective*), regardless of the direction of these

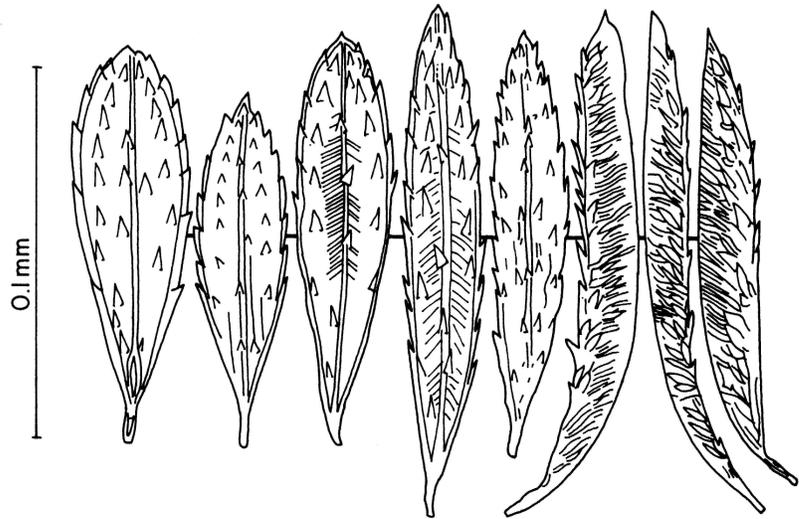


Figure 1. Representative scales from the dorsal opisthosoma of *Anasaitis canosa*, captured in Marion County, Florida, in 1976. Scale colors as viewed through a compound microscope at 1000x with oil immersion were: (left to right) white to silver to copper granular, light brown granular (gold iridescent), red-brown clear (gold iridescent), yellow-green clear, olive clear, olive clear, colorless clear (silver), and red-brown clear. The first five scale types (left) were flattened with adnate spines. The others were laterally compressed.

secondary objectives relative to the direction of the prey or primary objective, is reviewed.

3. Introduction

The jumping spider *Anasaitis canosa* is one of the most common salticids encountered in the forest floor, leaf litter habitat in the southeastern United States. These small spiders (5mm or less in length) are relatively easy to recognize as they move their pedipalps up and down, each marked with a bright white patch of scales. *Anasaitis* is a largely Neotropical genus of spiders that are widely distributed in the Caribbean. This genus is characterized by many colorful, iridescent, flattened scales on the body (Edwards 1999, Hill 1979b, see also Figure 1).

Earlier students of this spider's behavior (Edwards 1974, as *Stoidis aurata*, Jackson and van Olphen 1991, as *Corythalia canosa*) have described how they feed upon ants. Edwards systematically tested the tendency of these spiders to prey upon a wide range of different ant species in Florida. He described the careful approach of *Anasaitis*

canosa to larger ants, as compared to a less discriminating approach to smaller ants. In the present paper, only pursuits of relatively small, fast-moving brown forest ants (species not known) were observed.

Salticid spiders frequently demonstrate their strong capability to complete a non-linear or even circuitous route in pursuit of sighted prey, or in pursuit of a sighted target position. Although there were many earlier students of these spiders, Bilising (1920) may have provided the first documented account of this behavior, with respect to the salticid *Phidippus audax* in pursuit of a grasshopper. Later, Heil (1936) reported the similar abilities of several species of *Evarcha* to complete detoured or circuitous pursuits, and referred to these abilities as the *hohere Leistungen* of these spiders. My first field observations of the navigation of the salticid *Eris militaris* (*E. marginata*) took place in Oregon's Willamette Valley during the Spring of 1975 (Hill, 1978a):

At times individual E. marginata appear to wander greatly, without apparent destination. They may also, however, maintain a fairly constant course when moving through vegetation. While maintaining such a course, the animals may periodically stop to survey an elevated (highly visible horizon marker) "objective" plant, then continue the advance. Thus they may travel more or less directly toward what may be a rather distant goal. At times the spiders consistently ascend as they climb or jump from leaf to leaf. Often they will survey a position with the AME [anterior medial eyes], and then employ an indirect route to attain that sighted position, as necessitated by the arrangement of branches and twigs. Visual survey plays a primary role in the determination of a course by Eris.

In August of 1976, I completed extensive field observations of the behavior of immature *Phidippus princeps* (Hill, 1977), which included a number of observations of the indirect pursuit of either prey or positional objectives (e.g., pursuit shown in Figure 2). This was followed by a series of laboratory experiments which demonstrated the ability of a number of different species of *Phidippus* jumping spiders to utilize the route, distance, and direction of movement, visual cues, and the Earth's gravitational field to maintain a memory of direction and relative position during movement toward sighted objectives (Hill 1978b, Hill 1979a).

More recently, R. R. Jackson and his associates, in a series of papers (Tarsitano and Jackson 1992, Jackson and Wilcox 1993, Tarsitano and Jackson 1994, Tarsitano and Jackson 1997, Tarsitano and Andrew 1999) described detoured routes used during the pursuit of prey by salticids of the genera *Portia*, *Trite*, *Euryattus*, *Euophrys*, and *Marpissa*. Thus it should come as no surprise that a ground-dwelling spider such as *Anasaitis* should also



Figure 2. Detoured pursuit of a fly by an immature *Phidippus princeps* (based on detailed field sketch as figured in Hill 1977 and Hill 1978b). From a waiting position under a *Solidago* leaf (1), the spider turned rapidly (2) to face a fly (F) that alighted on a nearby stem of *Euphorbia esula*. The spider ran down the underside of the leaf (3), then stopped and reoriented to the position of the fly (4). The spider then ran down to the *Euphorbia* (5), and rapidly turned to look back up at the fly again (6). Then the spider climbed quickly through the *Euphorbia* leaves before reorienting once more (8) to the position of the fly. At this point the fly flew away.

exhibit the ability to negotiate complex routes of indirect pursuit.

4. Materials and methods

In October of 2005, a series of *Anasaitis canosa* spiders were filmed with a small, hand-held digital camera, producing Quicktime™ movies at the relatively low resolution of 320x240 pixels (30fps). In each case, the camera was held directly overhead, at a distance of about 25cm from the subject, during filming. The field of view at this distance was approximately 10cm in width. Individual frames from these movies were captured and cropped to assemble the photomontages depicted in this report. Two representative pursuits, each of which resulted in the successful capture of an ant, were selected for presentation. All filming took place in the Woods at Neely Farm, a mixed but primarily deciduous oak (e.g., *Quercus falcata*) woodland just west of Simpsonville in Greenville County, South Carolina. MPEG-1 movies of each of these pursuits can be obtained upon request from the author.

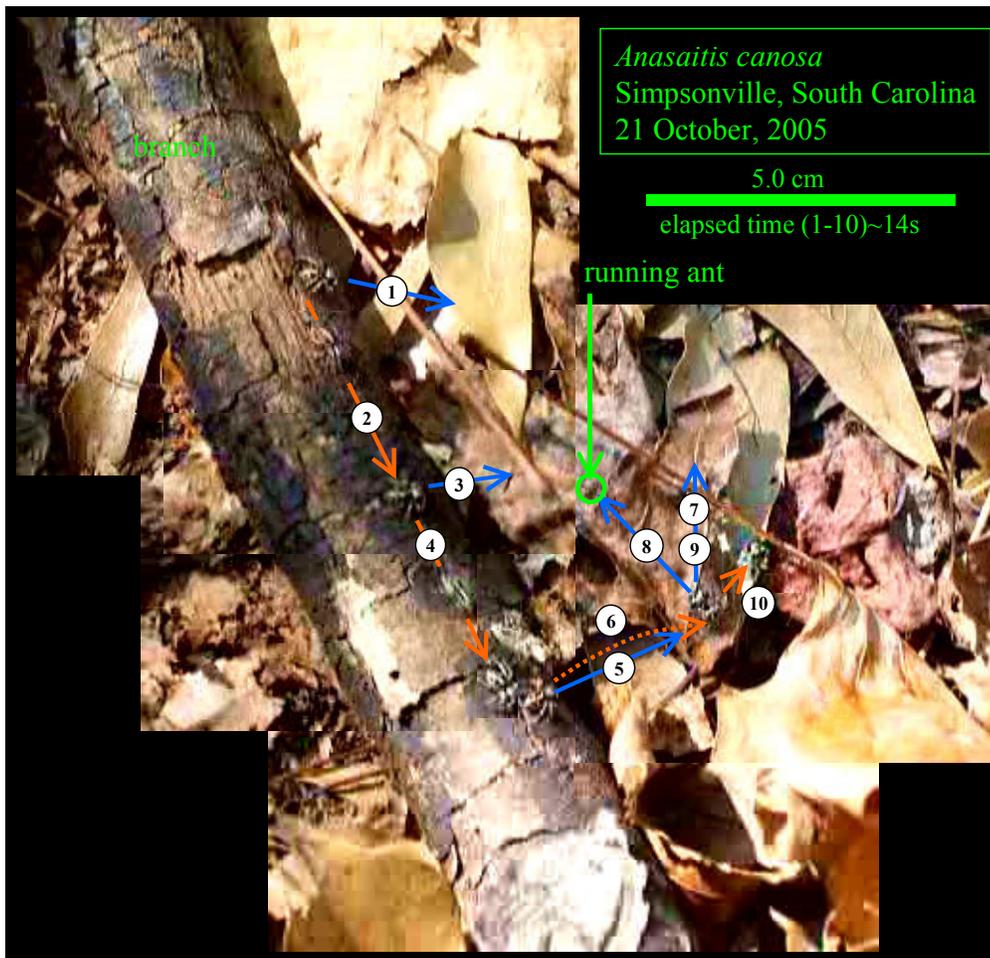


Figure 3. Interception and capture of running ant by *Anasaitis canosa*. The spider first turned quickly to face the moving ant (1), then ran quickly along the top of a horizontal branch lying on the ground (2). A rapid reorientation turn (3) was followed by continued pursuit along the top of the branch (4), followed by a turn to face a nearby leaf (5) and a jump to that leaf (6). At this position, the spider reoriented again (7), then turned to face the moving ant when it reappeared (8, *running ant*). The spider turned back to its earlier orientation (9) after the ant disappeared under a leaf (to the right of the running ant position marked above). When the ant reappeared from under this leaf, to the right, the spider turned quickly and jumped on the small ant to capture it (10).

5. Results

The two successful pursuits are described in Figures 3 and 4. In each case, the subject of pursuit was a rapidly running, small forest ant (best seen in the inset picture in Figure 4), of unknown species.

The first pursuit (Figure 3) demonstrated the use of a horizontal branch as a rapid route of access, as well as the ability of an *Anasaitis canosa* spider to intercept a rapidly running ant by moving quickly past the sighted position of the ant to a position closer to the ant where the spider could wait for the ant to reappear.

A horizontal branch was also used by an *A. canosa* spider in the second pursuit (Figure 4), in which the spider compensated for movement down and to the right (positions 2 to 5) by subsequent movement up and to the left (positions 6 to 8), to rapidly attain a position close to where the prey had been sighted, at a distance exceeding

10 cm. In this case, the spider also demonstrated the ability to move quickly and then to wait (position 17) for reappearance of the rapidly moving ant.

6. Discussion

Detoured or indirect pursuit by Anasaitis

The ability of *Anasaitis canosa* to rapidly approach a sighted prey position and then to wait for the prey to reappear is well-suited for its capture of rapidly running ants. Basic features of this pursuit, including the use of sighted intervening or secondary objectives (e.g., the leaf sighted in Figure 3 at position 5, or the branch that the spider jumped to in Figure 4 at position 4), the use of reorientation turns to face the expected position of the prey after movement to a new position (e.g., positions 3 and 7 in Figure 3), and continuation of the pursuit when the prey is out of sight, agree with the basic features of pursuit described previously for jumping

spiders of the genus *Phidippus* (Hill 1977, 1978b, 1979a).

While *Phidippus* frequently employ waiting positions on the stems of herbaceous plants as vantage points from which prey can be sighted, it appears that the ground-dwelling *Anasaitis canosa* spiders can employ large branches or logs as vantage positions that emerge from the confusion of surrounding leaf litter. These branches can also serve as pathways for rapid access to sighted prey.

Intelligence of salticid spiders

A high degree of *intelligence* can be attributed to the behavior of salticids, in large part because they are visual predators (which we, as visual animals, can relate to), with extraordinary development of visual acuity and visual centers of the syncerebrum. This is appropriate, to the degree that we understand that intelligence is a reflection of the ability of these animals to process large

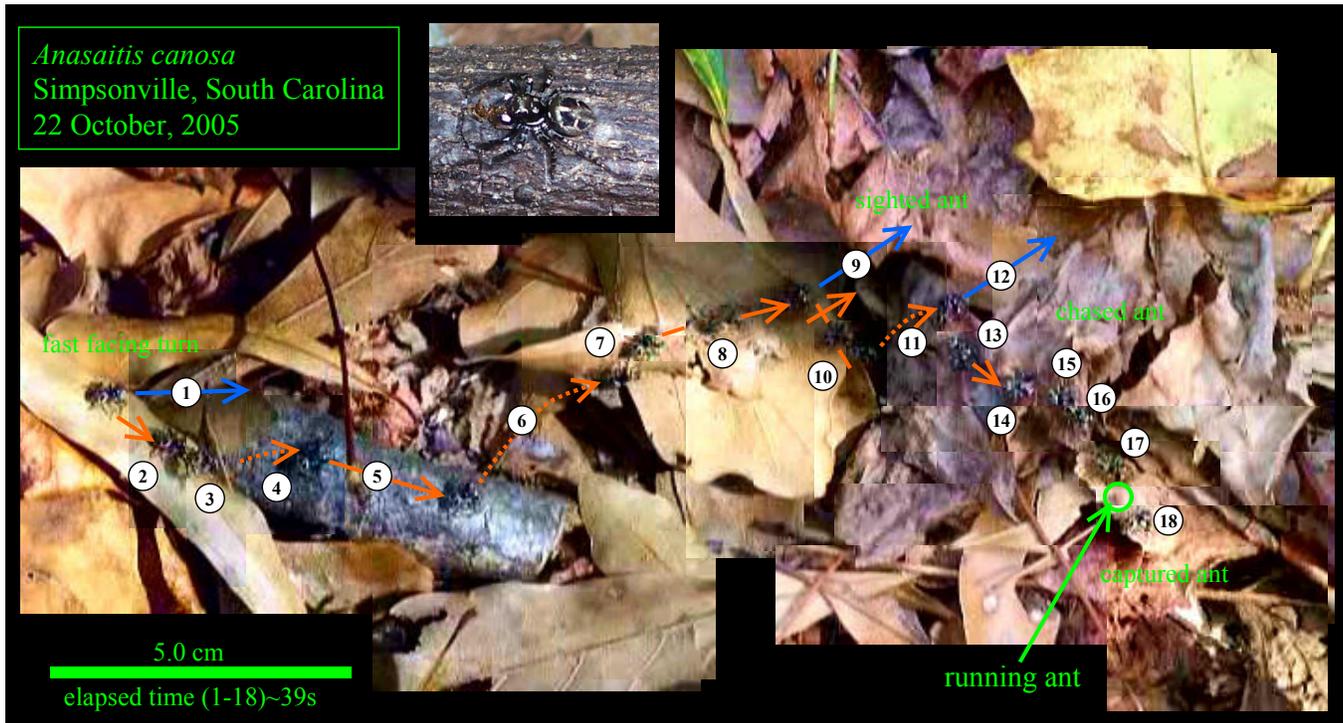


Figure 4. Longer pursuit of a sighted ant by *Anasaitis canosa*. The spider turned quickly to face the moving ant (1) at a distance of more than 10cm (sighted ant). This was followed by a very fast, uninterrupted, run (2 to 3), jump down to a horizontal branch on the ground (4), run along the top of that branch (5), jump back up to a leaf (6), and run along the top of that leaf (7 to 8) to a position where the ant was seen again (9). In pursuit of the ant, the spider then side-stepped along a leaf (10), jumped up to another leaf (11, facing direction 12). In rapid pursuit of the running ant (13-16), the spider reached a position at which it waited briefly (17) until the ant reappeared and could be captured (18). The inset picture (top) shows a close-up of this spider feeding on this ant, after it had moved back to a different position on top of a nearby horizontal branch.

amounts of information, and to behave, as a result, in a meaningful way. Of course the same can be said of animals that are less visually oriented, including many spiders which exhibit other kinds of extraordinary intelligence. We should be wary of the depiction of salticids alone among spiders as extraordinarily gifted, or even the behavior of specific groups of salticids as unique. At this point, very few salticid spiders have been observed in detail, and many surprises await us.

Recently the use of the term *cognition*, based upon its application in cognitive psychology, has come into vogue with respect to the description of the behavior of other animal species, including salticids. Unfortunately, this term is loaded with many connotations with respect to our private and subjective human experience and perception (as extended to our understanding of the behavior of other human beings), and the danger is always present that we will use our subjective experience of perception and purposive action to interpret animal behavior in a manner that is not warranted. Even our language can make it difficult to describe animal behavior in a truly objective manner. For example, when we say that a spider chases an ant *so that it can feed on it*, we are suggesting the presence of a purpose that may be implicit in the evolved behavior of the spider, but the same may not actually figure into the perception or the thought processes of the spider during the chase.

With more specific reference to the observations reported here, *Anasaitis canosa* has apparently evolved a behavior that allows it to intercept rapidly moving ants, but we cannot conclude that these spiders have the thought, intention, or perception (cognition) of *intercepting an ant* when they do this.

Note that *this is not to say that a spider does not have subjective experience, or mind*, or that the spider functions as an *automaton*. Indeed, there much evidence from observed behavior that a spider is subject to motivational mechanisms akin to pleasure and pain, and that a spider also functions at the level of execution of basic concepts (generalized or context-forming objectives, or other *representations* as described by Schomaker 2004) in its behavior. We simply do not have many tools to venture beyond the safety of a conservative behaviorist approach at the present time, and need to be wary.

One very interesting and relatively recent development involves the application of methods that I applied to the study of salticid orientation (Hill 1978b, Hill 1979a) to the study of human behavior, with very similar results (Philbeck, Loomis, and Beall 1997). The authors introduced the term *triangulation by walking*, and reported that the *visually perceived location* of a target at the start of movement, along a route that did not lead directly to that target, was systematically maintained and updated by human subjects during movement along that

route, and was subsequently used as they attempted to move, with eyes closed, toward that target. The authors of this study presented their hypothesis that use of this *internal representation of location* is a normal feature of human behavior, even when subsequent visual cues are available during movement. There is good reason to believe that the internal representation of location by salticids and many vertebrates (including humans) is evolutionarily convergent and highly analogous in function.

Movement toward secondary objectives

In earlier work (Hill 1978b, Hill 1979a), I presented the view that salticids could complete long and complicated detours in pursuit of a target (*primary objective*) through the completion of step-wise pursuit of a series of intervening or *secondary objectives*. As the examples presented here suggest, it was easy to observe that *Anasaitis canosa* spiders, like other salticid spiders, could visually identify and then move to a branch or a leaf, or a series of these facilitating positions, within the larger context of pursuit. As long as the spider can continue to calculate the relative direction and distance of the primary objective as it moves, there is no reason to evoke a more complicated mechanism for the observed ability to complete a longer or more complex pursuit sequence. All evidence suggests that these spiders observe and react to *what can be seen in their immediate environment* very quickly during pursuit.

I do not presently have access to reported experimental results suggesting that a *Portia* jumping spider can study a complex situation and plan out a complex route of pursuit in advance (Jackson and Wilcox 1993, page 138). For a spider like *Portia* that frequently pursues stationary prey, this remarkable ability would be of some use, particularly since the orientation of the web itself may be critical to safe and successful capture of a resident araneid spider. The situation is different for many salticids, such as *Anasaitis canosa*, when they pursue rapidly moving prey that quickly disappear from view. In the latter case, *time is of the essence*.

Movement away from prey during pursuit

Tarsitano and Jackson (1994) coined the term *reversed-route detour* to describe the case where a salticid moved away from the primary objective during pursuit. This was distinguished from the term *forward-route detour* which apparently described movement that shortened the distance between the spider and its primary objective.

In the pursuit shown in Figure 3, the *Anasaitis canosa* spider moved past the prey position and further away from the prey during the second segment of pursuit (run 4 after reorientation 3), thus attaining a position from which it could jump to a nearby leaf and intercept the running

ant (completing a nearly 180 degree reorientation to position 7).

Despite the claim of novelty related to the observation of *reversed-route detours* in a report by Tarsitano and Jackson (1994), that capability had already been extensively depicted in earlier work, in both horizontal and vertical planes of pursuit (e.g., Figure 5 in Hill 1977, Figures 5-12, 23-27, 59, 67, 68, 92-95, 111-115 in Hill 1978b, Figures 1, 2, 10, and 11 in Hill 1979a). In fact, Heil's earlier (1936) descriptions featured movement away from the prey position during pursuit by *Evarcha* jumping spiders. My earlier reference (Hill, 1979a) to movement toward a *visually determined secondary objective* was not intended to impose any limitations on the direction of a secondary objective relative to the direction of a primary objective, contrary to the interpretation of Tarsitano and Jackson (1994, top of page 67).

Incidence of detouring in invertebrates and vertebrates

Jackson and Wilcox (1993) quoted a statement by Curio (1976) that the ability to complete a detour in the pursuit of prey is a rare behavior among invertebrates. There may be little support for this assumption, and it is difficult to *disprove* the existence of a capability in any case. The sophisticated mechanisms of spatial orientation or *path integration* that have been demonstrated in many arthropods (e.g., *Araneus*, Vollrath, Norgaard, and Krieger 2000, *Uca*, Layne, Barnes, and Duncan 2003, *Cataglyphis*, Wolf and Wehner 2005, and the sparassid *Leucorchestris*, Norgaard, Henschel, and Wehner 2006), or the ability of mollusks to utilize indirect routes (e.g., *Octopus*, Mather 1991, and *Anguispira*, Atkinson 2003) suggest that similar abilities may be of widespread occurrence, if we look for them in the appropriate context.

Certainly an analogous capability has been demonstrated in many vertebrates (e.g., *Bufo*, Collett 1982, *Mus*, Bardunias and Jander 2000, and *Canis*, Cattet and Etienne 2004).

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