



# Startle Responses of Jorō Spiders (*Trichonephila clavata*) to Artificial Disturbance

Andrew K. Davis \* and Amitesh V. Anerao

Odum School of Ecology, University of Georgia, Athens, GA 30602, USA

\* Correspondence: akdavis@uga.edu

**Abstract:** The jorō spider (*Trichonephila clavata*, originally from east Asia) has been introduced in the southeastern United States, and is rapidly expanding this range, leading to questions about what facilitates this spread. Meanwhile, its cousin, the golden silk spider (*T. clavipes*), already has a range that covers most of the southeast. In an ongoing effort to understand the behavior of jorō spiders in their introduced range, we undertook the current project to evaluate how they react to perceived threats, which can inform us on how a species interacts with conspecifics, or how well it can tolerate anthropogenic disturbances. We collected mature females of both *Trichonephila* species, plus three locally common orb-weaving species in Georgia, and we evaluated the time spent immobile after experiencing a mild disturbance (a brief puff of air). We also collected similar “air puff response” data for five other North American species from the published literature. Collectively, the dataset totaled 453 observations of freezing behavior across 10 spider species. Comparing these data across species revealed that most spiders remained immobile for under a minute after the stimulus. Meanwhile, both *Trichonephila* spiders remained immobile for over an hour, which appears to be unprecedented, and suggests that spiders in this genus are the “shyest” ever documented. This reaction could also allow *Trichonephila* spiders to tolerate urban environments by remaining motionless throughout each disturbance instead of fleeing.

**Keywords:** jorō spiders; golden silk spiders; *Trichonephila clavata*; *Trichonephila clavipes*; behavior; disturbance



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## 1. Introduction

Non-native species can cause economic and environmental problems in their introduced range. Arthropods such as spiders are no exception [1–3], and in fact, their sessile nature makes them easily transported globally within shipments of fruit or other materials in commerce [3]. This is likely the reason for the introduction of the “jorō spider”, *Trichonephila clavata* (Figure 1), in northern Georgia, USA, in 2013 [4]. This orb-weaving spider is native to eastern Asia and Japan, and was thought to be transported to the U.S. on a shipping container [4]. As of October 2022, *T. clavata*’s range spans at least 120,000 km<sup>2</sup> [5], and it has been found in all neighboring states of Georgia. This rapid colonization engenders many questions about how this species can so readily adapt to new territories and environments. Based solely on its range expansion, one could reason that these spiders might have some innate aggressiveness that gives them a competitive advantage over native spiders. This was the question tackled in the current project.

Ironically, the large size and striking nature of jorō spiders makes their spread easy to track via public observations. Webs of this species are exceptionally large (1–2 m diameter) and can be found on bushes, trees, and human dwellings. In fact, the species appears to be highly tolerant of human-modified landscapes (Davis, *pers. obs.*). Occasionally, multiple webs can be found in the same location, with dozens of webs connected by support strands, all forming a “colonial” web (Davis, *pers. obs.*). This same opportunistic colonial behavior has been observed in its native range of eastern Asia [6]. Its cousin, the golden silk spider

(*T. clavipes*, Figure 1) has a range that includes most of the southern U.S. and beyond, into Central America [7]. Records of this species in the United States date back to the 1800s [8], and its large range now also implies an ability to successfully colonize new territory. It, too, is capable of forming opportunistic colonial webs [9–11], which highlights certain behavioral consistencies within this genus.

Since our lab is located in northeast Georgia, we have been endeavoring to understand the biology of jorō spiders in this introduced range, including by evaluating how their physiology allows them to live in a more temperate climate than their golden silk spider cousin [7]. We have also recently reported how the physical strength of jorō spider webs is far beyond that of native species' webs [12]. Here, we describe results from a simple laboratory experiment which was designed to test if jorō spiders differ, in terms of disturbance reactions, from other spiders that are native to (or that have ranges in) North America. We reasoned that the results from this test would help to identify any behavioral traits (i.e., such as boldness) that would aid their successful colonization of the non-native ecosystem.

Specifically, we evaluated the jorō spiders' behavioral responses to threats by timing their thanatosis (freeze response) reactions to a mildly stressful stimulus, i.e., a puff of air [13]. Such air puff tests have been employed in other investigations of spider behavior, because the duration of thanatosis is a good proxy for the perceived threat level and/or the individual behavior of the spider [14]. Spiders that remain in a thanatosis state for longer are thought to be “shyer”, while those that show little or no reaction are thought to be more “bold”. For comparison, we also evaluated the thanatosis reactions of the golden silk spider, which, if similar, would indicate a shared trait within the genus. We also collected similar behavioral data on three spider species from the local area, plus we collated similar published data on five other species that are native to, or have ranges within, North America.



**Figure 1.** (Left): Jorō spider, *Trichonephila clavata*, photographed in Oconee County, GA, USA, on 3 October 2022. (Right): Golden silk spider, *T. clavipes*, photographed in Richmond County, GA, USA, on 30 September 2022. Both photographs taken by A. Davis.

## 2. Materials and Methods

**Spider collection**—This project was conducted during the fall (2021), which is when the majority of orb-weaving spiders in our region have established webs and female spiders are large and mature. Female spiders were collected by pulling down their webs with a stick and placing them in 50 mL falcon tubes. They were collected the day before each trial, and housed in our lab overnight (in their falcon tubes) in a 10C fridge. They were removed from the fridge 1 h prior to trials. We collected a total of 16 jorō spiders from nearby locations around the University of Georgia (Clarke County) in October 2021. We collected 15 golden silk spiders, *Trichonephila clavipes*, near Augusta, GA (Richmond County). We also collected 17 garden spiders (*Argiope aurantia*), 10 banded garden spiders (*A. trifasciata*), and 6 marbled orb weaver spiders (*Araneus marmoreus*) from Clarke and Oconee County, GA, to use in the study.

**Disturbance trials**—These trials were designed to observe the thanatosis (freezing) behavior of spiders, which is a common reaction by spiders when faced with a threat [13]. Each spider was placed in an empty white plastic container (30 cm × 50 cm) and allowed 1 min to explore the container. The walls of the container were high enough so that they could not climb out (see Video S1 in Supplementary Materials). Then, one of us (AVA) used a 20 cm long turkey baster to gently blow two rapid puffs of air onto the spider, approximately 5 cm from its cephalothorax. After the puffs, we recorded the duration of time (in seconds) each spider remained immobile, which was the parameter of interest.

We conducted these trials on individuals of the two *Trichonephila* species, plus three other orb-weaving species that were collected locally (Table 1). To supplement these data, we also gleaned similar data from an additional 5 spider species from the published literature, i.e., from studies where air puff tests had been conducted, and where raw data had been provided, either in graphs within the papers, or as supplemental materials (see Table 1). Each of these studies involved some measure of thanatosis after the air puff, either in the form of a spider retreating and huddling in its funnel, as in the case of the two studies of *Agelenopsis* spiders [15,16], or where spiders simply huddled in place [17,18]. In some studies, spiders were tested on their own webs [15,16], while in others, they were removed and placed on a tray for testing [18]. Importantly, while the procedures in these studies differed, the fact that the outcomes were similar (see Section 3) argues that they should be comparable to our own data, regardless of any procedural differences.

**Table 1.** Summary of data and sources used to compare startle reactions of spiders. Published data were either extracted from graphs provided in papers, or from raw data provided in supplemental files of papers.

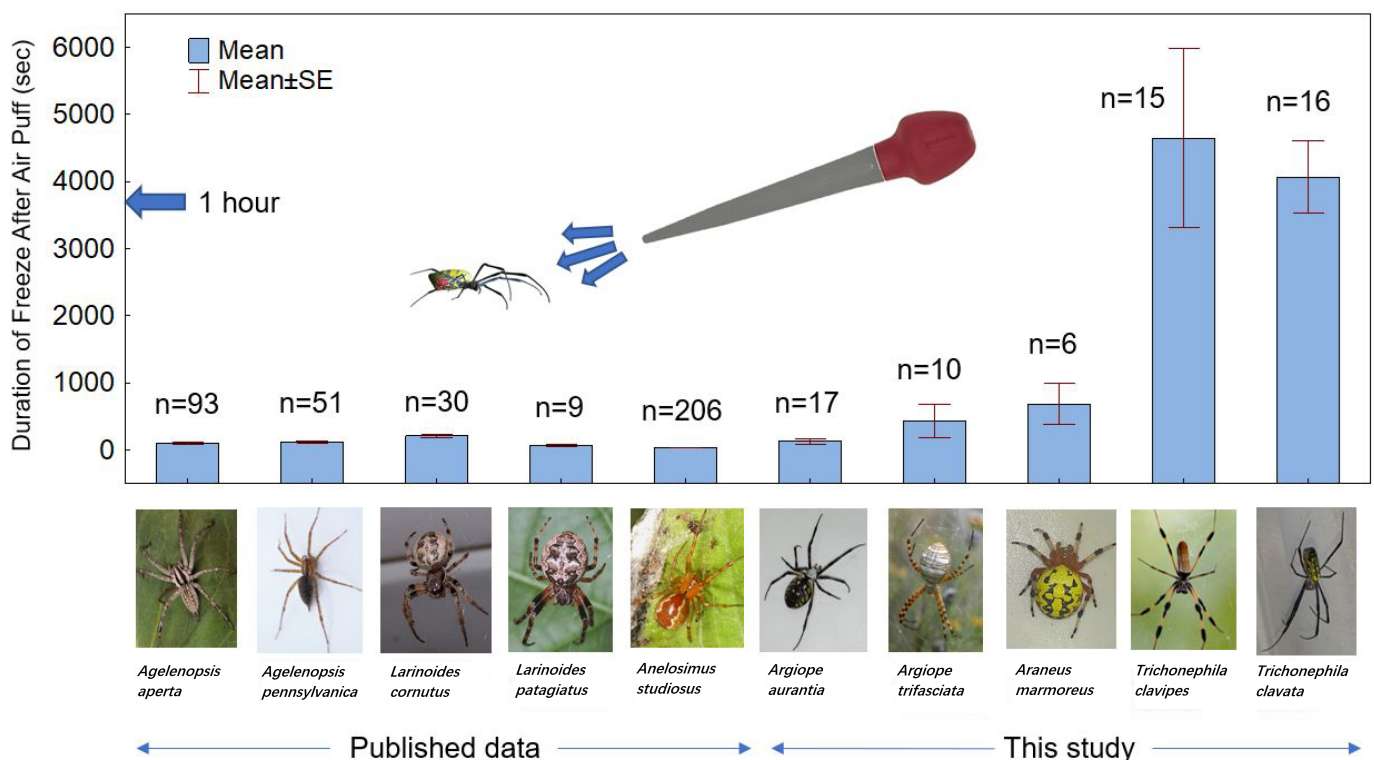
Spider Species	# Spiders Tested	Source
Funnel-web spider ( <i>Agelenopsis aperta</i> )	93	[15]
Pennsylvania grass spider ( <i>Agelenopsis pennsylvanica</i> )	51	[16]
Communal spider ( <i>Anelosimus studiosus</i> )	206	[17]
Furrow orb spider ( <i>Larinoidea cornutus</i> )	30	[18]
Ornamental orb weaver ( <i>Larinoidea patagialis</i> )	9	[18]
Marbled orb weaver ( <i>Araneus marmoreus</i> )	6	This study
Banded garden spider ( <i>Argiope trifasciatus</i> )	10	This study
Garden spider ( <i>Argiope aurantia</i> )	17	This study
Golden silk spider ( <i>Trichonephila clavipes</i> )	15	This study
Jorō spider ( <i>Trichonephila clavata</i> )	16	This study

Collectively, our combined dataset amounted to 453 observations of thanatosis behavior across 10 spider species. In all cases, the unit of replication was the measure of

thanatosis duration (in seconds). These data were log transformed (+1) to approximate normal distributions, and we then used ANOVA to determine if the thanatosis time differed across species. Since sample sizes were uneven across species, we weighted this analysis based on sample size; species with 10 or fewer data points were weighted as '1', those with more than 10 but fewer than 50 were weighted as '2', and those with more than 50 were given a '3' weighting score. Statistical analyses were performed using the Statistica 13.5 software package (Tibco Software, Inc., Palo Alto, CA, USA).

### 3. Results

Across all non-*Trichonephila* spiders, including the three species that we tested in our lab, plus the five from the literature, the average time in a thanatosis state after the air puff was 96 s ( $\pm 203$  s). Meanwhile, jorō spiders tended to remain frozen for over 1 h in most cases; the average duration from 16 spiders was 4068 s ( $\pm 2167$  s), or about 67 min (Figure 2). We are confident in this assessment, since the jorō spiders all showed the classic signs of thanatosis (immobile, no leg or body movement), and the end of the behavior was also easily recognized (abruptly resumed movement). Furthermore, their thanatosis state was not visually dissimilar to that of the three other orb-weaver species we tested. The shortest interval of all jorō spiders was 11 min, which was still 7 times longer than the average for the other spiders. No jorō spiders failed to display a thanatosis reaction. Similarly, the golden silk spiders tested also remained frozen for over an hour, and again, all individuals reacted. The weighted ANOVA test revealed significant variation in means across all spider species ( $F_{9,1221} = 95.66$ ,  $p < 0.001$ ), and a Tukey's post hoc test indicated that the two *Trichonephila* species differed significantly from all others but did not differ from each other ( $p < 0.01$ ).



**Figure 2.** Behavioral responses of spiders to a mild disturbance stimulus (air puff), from our tests, plus from data presented in published studies (see Table 1). Shown are the mean durations of time spent in a “thanatosis” state after receiving the stimulus.



#### 4. Discussion

In this study we sought to determine if non-native jorō spiders differed from other spiders in North America in one aspect of their behavior, their reaction to perceived threats (in this case, a puff of air). This same “air puff test” is often used to evaluate the boldness behavior of spiders [15,19,20], and it is generally thought that longer bouts of freezing reflect a “shyer” personality. Conversely, spiders that display little to no freezing behavior are thought to be bolder and/or more aggressive. Some spider researchers refer to this reaction as a “startle response” and may even elicit the reaction by other means, but the duration of the freezing afterward is interpreted in the same way [21]. In fact, regardless of the means of inducing the reaction, this interpretation is consistent across studies of other arthropods [22–24].

Going into this experiment, we had little background information on jorō spider behavior upon which to form expectations of the outcome, though given their rapid range expansion in the United States, one could easily conclude that this species must have an aggressive or bold personality (i.e., allowing it to outcompete native spiders, and/or successfully colonizes new territory). Surprisingly, we discovered the opposite was true. In our standardized laboratory trials using a simple air puff test, we found that the reactions of jorō spiders, plus their *Trichonephila* cousin, both had an extremely prolonged reaction (Figure 2), which points to an extremely shy and non-aggressive personality. We are quite certain of this finding; their frozen state did resemble that of the other species (visually), but they remained in this frozen state for over an hour, while most other species usually resumed ambulatory activity after 1–2 min. Moreover, the fact that the three non-*Trichonephila* species we tested showed no prolonged reaction argues that the procedures used here (collection, storage of spiders, materials used, etc.) did not artificially produce these findings. In fact, we ourselves were surprised when conducting the tests because the reactions of the *Trichonephila* spiders differed so greatly from the published literature. In fact, based on a thorough review of the relevant literature, we could find no other published record of a spider species with such a lengthy startle reaction (i.e., over 1 h long). Since both *Trichonephila* species displayed a similar startle response, we hypothesize that this prolonged response must be an innate trait of this genus.

It is unclear why spider in the genus *Trichonephila* would have such an extremely shy and non-aggressive personality. The prolonged response to perceived threats could be a unique form of defensive strategy within these species that has evolved because of the heightened level of predation within colonial webs compared to solitary webs [25]. Recall that both *Trichonephila* species can exist in a solitary web, or in a larger, communal web [6,10]. Colonial webs are inherently more “apparent” to aerial predators, and so spiders in the colony must face a heightened predation risk, though the sheer number of individuals does provide predators with more choices, thereby lessening the individual risk [9]. In theory, when aerial predators attack spiders in colonies, all members of the colony are aware of the threat, so remaining frozen for this duration could lessen the risk of detection when the predator is present and “foraging” at the web cluster. However, this explanation does not fit with all of the evidence gathered here; one other species included for comparison (*Anelosimus studiosus*) has a similar flexible lifestyle, existing solitarily or colonially, and its startle response was not unusually long (Figure 2).

Another possible explanation is the body size of the spiders; both *Trichonephila* spiders are large, and one could reason that larger-bodied spiders might simply be slow-moving. In a prior study, the average body mass of 34 mature female *T. clavata* was 0.67 g ( $\pm 0.34$  sd), and for 23 *T. clavipes* it was 1.45 g ( $\pm 0.43$  sd) [7]. However, consider that we ourselves tested the startle responses of two other large-bodied *Argiope* species in this study. The body mass of the 17 mature, female garden spiders in this study, for example, was 1.03 g ( $\pm 0.56$  sd). The fact that the *Argiope* spiders were of similar size but did not display a prolonged startle reaction as well, argues that body size is not the causative factor here.

One could also consider that this prolonged thanatosis state is somehow related to the physiology of the *Trichonephila* genus, and these spiders may have a slower metabolism,

which slows their movements. We can also rule out this explanation. Prior work in our lab actually evaluated the oxygen consumption rates of both species [7], which were  $\sim 375 \mu\text{LO}_2/\text{g}/\text{h}$  and  $\sim 175 \mu\text{LO}_2/\text{g}/\text{h}$ , respectively. While *T. clavipes* does have a lower rate than *T. clavata*, compared to the reported values for other spiders e.g., 43–356  $\mu\text{LO}_2/\text{g}/\text{h}$  [26], neither can be considered exceptionally low.

While the exact mechanism behind the species' differences in startle responses is unknown at this time, these results could help to explain the rapid range expansion of the jorō spider in its introduced range, and especially its clear affinity for inhabiting urban landscapes. Our location in northern Georgia is close to the epicenter of the jorō introduction [4], and here, the species seems to be thriving, especially in the city of Atlanta. Ten years after they were first sighted, the number of jorō spider webs in this epicenter now easily numbers in the millions, and the spider is quickly expanding its range into neighboring states. We believe that the unique disturbance reaction of this species, plus its *Trichonephila* cousins, could be an explanation for how they can thrive in human-dominated landscapes, where they likely face a barrage of acoustic, vibrational, and visual stimuli on an hour-by-hour and perhaps minute-by-minute basis. Prior work has indeed shown how *T. clavipes* also appears unusually well-suited for exploiting heavily urbanized areas [27]; spiders living in urban areas were larger and had sturdier webs. Similarly, the related *Trichonephila plumipes* in Australia has been found to also grow larger with increased urbanization [28], which suggests that it, too, has an inherent ability to tolerate such environments. Subsequent investigations even labeled this species as “urban-tolerant” [29]. Meanwhile, similar research on the *Araneus diadematus* indicated a reduction in body size in urbanized areas [30], which signals how some spiders are less tolerant of these same anthropogenic disturbances. While there is little research so far on *T. clavata* in its introduced range, our anecdotal observations of it are consistent with the patterns observed in other *Trichonephila*; we have observed jorō spider webs in a wide variety of urban settings, including on gas station pumps, and even on traffic lights directly over busy road intersections (Davis, *pers obs.*). It is probably not a coincidence, then, that the *Trichonephila* species has such a unique reaction to disturbance, and that it is especially tolerant of city life. It may be that their prolonged freeze response allows them to avoid physically reacting to every minute-by-minute disturbance, and therefore save energy.

Finally, our study, and its surprising results, engenders a number of questions that could be explored in follow-up research. For example, future work should focus on understanding the physiological responses to stressful stimuli in *Trichonephila* spiders compared to other species, such as by measuring their heart rate before and after stress [31–33]. Additionally, it will be important to continue to study how jorō spiders in particular are able to inhabit and thrive in urban landscapes, which would help to predict the limits of its current spread in the United States.

## 5. Conclusions

In this study we evaluated the startle responses of jorō spiders in comparison with other species, including their cousin, the golden silk spider, in an effort to understand the behavior of this invasive species. After a mild stressor, both *Trichonephila* species displayed an exceptionally prolonged thanatosis reaction (over 1 h), compared to other spider species, which had reactions lasting for only minutes. This extreme thanatosis response appears to be unprecedented based on our survey of the relevant literature. This surprising behavior points to how members of this genus are exceptionally shy, which is noteworthy because spiders in this genus also have a unique tolerance of urbanized landscapes. Possibly this unusual form of reacting to stressors allows these spiders to tolerate the continuous disturbances that come with urban-living. Further research on this is warranted.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/arthropoda1020009/s1>, Video S1: Demonstration of the spider air puff test.

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