The influence of predator type on 'whirling' defensive behavior of *Pholcus ancoralis* (Araneae, Pholcidae), a tropical web-building spider

Theodore Striegel Corresp. 1

1 Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, California, United States

Corresponding Author: Theodore Striegel
Email address: tstriegel@berkeley.edu

Background. The 'whirling' defensive behavior of *Pholcus ancoralis* (L. Koch, 1865) was studied in a forest and laboratory in Mo'orea, French Polynesia. This behavior involves fast web-borne gyration to dissuade predators and is widespread in the Pholcidae family.

Methods. Different local predators (*Anterhyncium rufipes, Lipinia noctua,* and *Thorelliola ensifera*) were placed in two-chambered systems with *P. ancoralis* individuals and qualitative data on whirling frequency and duration were obtained.

Results. Potter wasps (*Anterhyncium rufipes*) triggered whirling in 50% of trials and moth skinks (*Lipinia noctua*) triggered whirling in 20% of trials. The average durations of the behavior triggered by each were 853 and 455 seconds, respectively. Pacific horned jumping spiders (*Thorelliola ensifera*) triggered whirling in 10% of trials with an average duration of only 20 seconds.

Discussion. Wasps triggered whirling the most frequently and of a long average duration. This has not been seen in other studied pholcids. This difference in predator specificity of whirling may be due to differences in habitat between pholcid species.

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2666v1 | CC BY 4.0 Open Access | rec: 21 Dec 2016, publ: 21 Dec 2016

The influence of predator type on ‘whirling’ defensive behavior of *Pholcus ancoralis* (Araneae, Pholcidae), a tropical web-building spider

Theodore Striegel
tstriegel@berkeley.edu

Department of Environmental Science, Policy, and Management
University of California, Berkeley
Berkeley, California
United States

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2666v1 | CC BY 4.0 Open Access | rec: 21 Dec 2016, publ: 21 Dec 2016

Abstract

Background. The ‘whirling’ defensive behavior of *Pholcus ancoralis* (L. Koch, 1865) was studied in a forest and laboratory in Mo’orea, French Polynesia. This behavior involves fast web-borne gyration to dissuade predators and is widespread in the Pholcidae family.

Methods. Different cohabiting predators (*Anterhyncium rufipes, Lipinia noctua,* and *Thorelliola ensifera*) were placed in two-chambered systems with *P. ancoralis* individuals and qualitative data on whirling frequency and duration were obtained.

Results. Potter wasps (*Anterhyncium rufipes*) triggered whirling in 50% of trials and moth skinks (*Lipinia noctua*) triggered whirling in 20% of trials. The average durations of the behavior triggered by each were 853 and 455 seconds, respectively. Pacific horned jumping spiders (*Thorelliola ensifera*) triggered whirling in 10% of trials with an average duration of only 20 seconds.

Discussion. Wasps triggered whirling the most frequently and of a long average duration. This has not been seen in other studied pholcids. This difference in predator specificity of whirling may be due to differences in habitat between pholcid species.

Keywords: Pholcidae, tropical spiders, predation, defensive behavior, whirling

Introduction

Defensive behavior is a strong determinant of the survival and reproductive success of an organism, and therefore of particular interest for its role in evolution. The most common response of prey is to remain motionless in the presence of a predator, although more complex behavior exists within the animal kingdom (Lima 1990). Research has found that many defensive behaviors are hardwired into the brains of prey (Blanchard 1990). Specific parts of the brain responsible for the fight-or-flight response have been mapped in mammals (Jansen *et al.* 1995). It is possible that analogues to these mammalian networks may be responsible for defensive behaviors in other organisms. Although less common, complex defensive behaviors are seen in small animals such as arthropods as well.

The defensive behavior of many silk-producing spiders centers around silk and the web (Tolbert 1975; Vetter 1980; Schoener 1992). The web is used as a substrate for defensive action (such as camouflage and escape) by many species. If defensive behaviors like these are hardwired, they must be the result of selective pressures (Blanchard 1990). This paper explores the specificity of these pressures. It is important to ascertain whether arachnid defensive behavior can be correlated with presence of specific predator types or if it is a general mechanism with no predator specificity.

The web-based defensive behavior of the Pacific cellar spider, *Pholcus ancoralis* (Araneae, Pholcidae), is a rarity within order Arachnida. In response to physical disturbance of its web, the spider initiates a period of intense vibration. It uses silk threads to pull its body in a circle at very high speeds (Jackson 1990). This so-called ‘whirling’ has been established as a defensive mechanism, elicited in response to proximity of certain predators (Jackson 1990, 1992; Heuts *et al.* 2001). The geographic range of *P. ancoralis* is restricted to Pacific islands (Beatty 2008). It is especially abundant on the Society Islands, the central island chain of French Polynesia (pers.

obs). On Mo'orea*,* *P. ancoralis* often builds webs on the *mape* (Tahitian chestnut, *Inocarpus fagifer*) trees that make up the majority of forest cover. It lays in the web with its abdomen oriented downwards, and moves quickly to dispatch any small insects that wander too close.

There is evidence that jumping spiders (family *Salticidae*) evoke whirling of a longer duration from *Pholcus phalangiodes* than that elicited by other tested predators (Huets *et al.* 2001). Variability in response time to different predators by members of this pholcid species, a cosmopolitan relative of *P. ancoralis*, lends credence to the idea that pholcid whirling is a predator-specific mechanism. This study aims to see if certain local predators induce whirling in *P. ancoralis* more consistently than others, to determine whether pholcid whirling is predator-specific.

Materials and Methods

Study site

Mo'orea, French Polynesia, is a highland island with a wet and tropical climate. Air temperatures on Moorea range from 20-30° C year-round. It features a mostly uninhabited interior covered in dense forest, within which all of the organisms used in this study cohabitate and interact. The Three Pines region of the forest-covered Opunohu Valley, Mo'orea formed the focal point of the study (Figure 1). The valley is dominated *by I. fagifer*, which provides dense canopy cover. *P. ancoralis* makes its web between the tall buttresses of the tree.

Selection of predators

Three different species of locally co-habiting predators were used. *Anterhyncium rufipes* (Hymenoptera, Vespidae, Eumeninae) is a tropical potter wasp, a predator of all smaller arthropods. Mature female Eumenids paralyze and collect small invertebrates to feed their larvae (Evans 1970). Wasps are the principle predator of pholcids (Bradley 2013). *Thorelliola ensifera* (Araneae, Salticidae) is a horned jumping spider that specifically targets *P. ancoralis* as prey (Chuang 2012*). Lipinia noctua* (Squamata, Scincidae) is the moth skink, a small lizard that preys upon a wide variety of arthropods. It is an opportunistic predator that feeds on various small invertebrates and has been observed targeting *P. ancoralis* (pers. obs. & Zughaiyir, obs., 2016).

Collection sites and methods

All specimens were collected manually, using 50-mL vials for the invertebrates and bare hands for the skinks. *Pholcus ancoralis, T. ensifera* and *A. rufipes* specimens were collected in the Three Pines region of the *mape* forest covering Opunohu Valley. *Pholcus ancoralis* and *T. ensifera* were randomly sampled from trees and rocks adjacent to or within five meters of trails. Mature *A. rufipes* females were only collected along the trail adjacent to archaeological site *Ahu-O-Mahine* (Mahine's Altar) due to prodigious local abundance*. Lipinia noctua* specimens were collected on the grounds of the Gump Research Station and the adjacent Atitea Cultural Center. Their confinement and use in the trials conformed to the guidelines established by the Animal Care and Use Committee at the University of California, Berkeley.

Experimental trials

Pholcus ancoralis individuals were allowed 2-3 days to establish dense webs in paper-towel lined 1-liter cups, and then subjected to a trial. In each trial, a predator individual was placed in another, unmodified, 1L cup and a two-cup complex was formed by taping the 1L cup that *P. ancoralis* had established in rim-to-rim with the predator cup. The complex was placed vertically with the *P. ancoralis* web-containing cup on top for all trials. Complexes involving *L. noctua* were supplemented with a 10-inch length of deadwood to enable climbing and proximal interaction with the pholcids.

Each species was evaluated with *P. ancoralis* in ten trials. Several preliminary tests involved pholcids kept in cup systems with no predator, left for 48 hours to ensure that the pholcids could endure this length of time in captivity in the absence of a predator. These tests standardized survivorship.

Variables measured in each trial included pholcid survivorship after 48 hours, and duration of any observed whirling. The trials were observed once an hour for five-hour periods on both the first and second day.

The statistical difference in duration of whirling between the trials involving each of the three predators was determined using a G-test performed using R (R Core Team, 2016) and the DescTools package (Signorell 2016).

Results

[Table 1]

Frequency of whirling triggered by different predators

Pholcus ancoralis whirled in 20% of trials when placed in a complex with a *T. ensifera* individual, as shown in Table 1. The average (mean) duration of this whirling was 20 seconds (sd = 0, n = 1). *Lipinia noctua* triggered whirling in 20% of trials, for an average duration of 455 seconds (sd = 639.92, n = 2). *Anterhyncium rufipes* triggered the most whirling by far, with 50% of trials displaying whirling that lasted for an average of 853 seconds (sd = 3123.34, n = 5). The difference in mean response times to each predator was found to be statistically significant (G test, $p < 0.05$).

In addition, two instances of long-duration whirling were observed in wasp trials (see Appendix 1). Huets *et al.* (2001) defined so-called ‘long-whirl’ as sustained whirling of more than ten minutes length, and often for two hours or more. Whirling lengths of ten minutes, and one hour, were recorded in two separate wasp trials.

Supplementary observations

Avoidance behavior, frequent movements to maintain proximity from the predator, was observed in all pholcids that were tested with *A. rufipes* and *L. noctua*, regardless of subsequent whirling. Most pholcids were calm around *T. ensifera*. Some pholcids were aggressive around *T. ensifera*, lowering themselves into the bottom cup shortly after the commencement of the trial and observing *T. ensifera* up close with occasional arm movements.

Anterhyncium rufipes rarely displayed interest in *P. ancoralis*, wandering around the cup system freely and coming within very close range of the pholcid, triggering whirling on many occasions with no change in the wasp's behavior. However, the occasions on which *A. rufipes* did display interest invariably ended in sustained whirling, and a surviving pholcid, or a paralyzed pholcid. *Lipinia noctua* paid little initial attention *to P. ancoralis* but in one trial was observed displaying hunting behavior within very close proximity of the pholcid. *Thorelliola ensifera* displayed cautious behavior when approaching *P. ancoralis*, with its body always oriented towards the pholcid. *Thorelliola ensifera* only came within a few centimeters of the pholcid for short durations, otherwise keeping its distance.

Contrary to the claims of previous literature (*i.e.*, Chuang 2012), *T. ensifera* appears to pose no threat to web-borne *P. ancoralis*. In 40% of trials, the salticid was killed and consumed by the pholcid. In only one trial did the opposite take place.

Pholcus ancoralis was documented aggregating off-trail in the study site. Very large, dense tangle webs containing up to seven mature individuals were observed. The individuals in these webs whirled in a semi-coordinated manner when one individual was disturbed. This behavior may be true colonialism, which is unreported in the *Pholcidae* family.

Discussion

The occurrence of long-whirl specifically in *P. phalangiodes*-salticid complexes led Heuts *et al.* (2001) to conclude that long-whirl in *P. phalangiodes* is specifically evoked by jumping spiders. In this study, the evidence points towards long-whirl in *P. ancoralis* being specifically evoked by wasps (Table 1). *Anterhyncium rufipes* triggered whirling more frequently than either *T. ensifera* or *L. noctua*, and evoked two instances of long-whirl. One instance of long-whirl was also observed in a pholcid-skink complex. It appears that whirling is indeed a predator-specific mechanism, selectively triggered by local predators that exert the most pressure on each *Pholcidae* species. The three predators tested with *P.* ancoralis in this study evoked whirling of significantly different durations. Whirling appears to be quite effective as a defensive mechanism; all pholcids who whirled during their trials also avoided predation, with the exception of one individual (see Table 1).

The unusual outcome of the pholcid-salticid complexes, high salticid mortality, may be due to study methodology. For example, Chuang (2012) did not provide the pholcids with anchor points for favorable web development; this may explain her greater reported pholcid mortality (when exposed to *T. ensifera*). A possible explanation is that *T. ensifera* habitually ambushes *P. ancoralis* when it is away from its web, however, this has not been corroborated through field observation.

Acknowledgements

I thank professors Cindy Looy, Ivo Dujinstee, Justin Brashares, Jonathon Stillman, and Patrick O'Grady for their guidance and ceaseless support. I also thank graduate students Ignacio Escalante, Natalie Stauffer-Olsen, and Eric Armstrong for hours spent transporting me to and from my field site and their excellent advice. Thanks to all my peers and the wonderful staff of the Richard B. Gump Field Station (Mo'orea, FP), who made this experience possible and incredible. Mauruuru!

References

Beatty JA, Berry JW, Huber BA. 2008. The pholcid spiders of Micronesia and Polynesia (Araneae, Pholcidae). *Journal of Arachnology* 36:1-25

Blanchard RJ, Blanchard DC, Rodgers J, Weiss SM. 1990. The characterization and modelling of antipredator defensive behavior. *Neuroscience and Biobehavioral Reviews* 14:463-472

Bradley RA. 2013. *Common spiders of North America.* Berkeley and Los Angeles: University of California Press.

Chuang A. 2012. Size and motherhood of the spider Pholcus ancoralis (Aranaeae: Pholcidae) affects whirling and other defensive behaviors. *Biology and Geomorphology of Tropical Islands*

Evans HE, West Eberhard MJ. 1970. *The wasps.* Ann Arbor: University of Michigan Press.

Heuts BA, Witteveldt M, Pires LD, van Wageningen F. 2001. Long-duration whirling of Pholcus phalangiodes (Araneae, Pholcidae) is specifically elicited by salticid spiders. *Behavioural Processes* 55: 27-34.

Jackson, RR. 1990. Predator-prey interactions between jumping spiders (Araneae, Salticidae) and Pholcus phalangiodes (Araneae, Pholcidae). *Journal of Zoology* 220: 553-559

Jackson RR. 1992. Predator-prey interactions between web-invading jumping spiders and two species of tropical web-building pholcid spiders, Psilochorus Sphaeroides and Smeringopus Pallidus. *Journal of Zoology* 227: 531-536

Jansen ASP, Van Nguyen X, Karpitskiy V, Mettenleiter TC, Loewy AD. 1995. Central command neurons of the sympathetic nervous system: basis of the fight-or-flight response. *Science* 270:644-646

Lima SK, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640

Schoener TW, Spiller DA. 1992. Stabilimenta characteristics of the spider Argiope argentata on small islands: support of the predator-defense hypothesis. *Behavioral Ecology and Sociobiology* 31:309-318

Starr CK. 2005. Defensive Whirling Behaviour in an Antillean Daddy-Longlegs Spider (Araneae: Pholcidae). *Living World, Journal of The Trinidad and Tobago Field Naturalists' Club* '2005':52-52.

Tolbert WW. 1975. Predator avoidance behaviors and web defensive structures in the orb weavers Argiope ornate and Argiope trifasciata (Araneae, Araneidae). *Psyche* 82:29-52

Vetter RS. 1980. Defensive Behavior of the Black Widow Spider Latrodectus hesperus (Araneae: Theridiidae). *Behavioral Ecology and Sociobiology* 7:187-193

Statistical software:

Signorell A et mult. al. 2016. *DescTools: Tools for descriptive statistics.* R package version 0.99.18.

R Core Team. 2016. *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. URL: https://www.R-project.org/.

Image credit:

UC Berkeley, with modification

Figure 1

Figure 1: The island of Mo'orea, with Three Pines area marked.

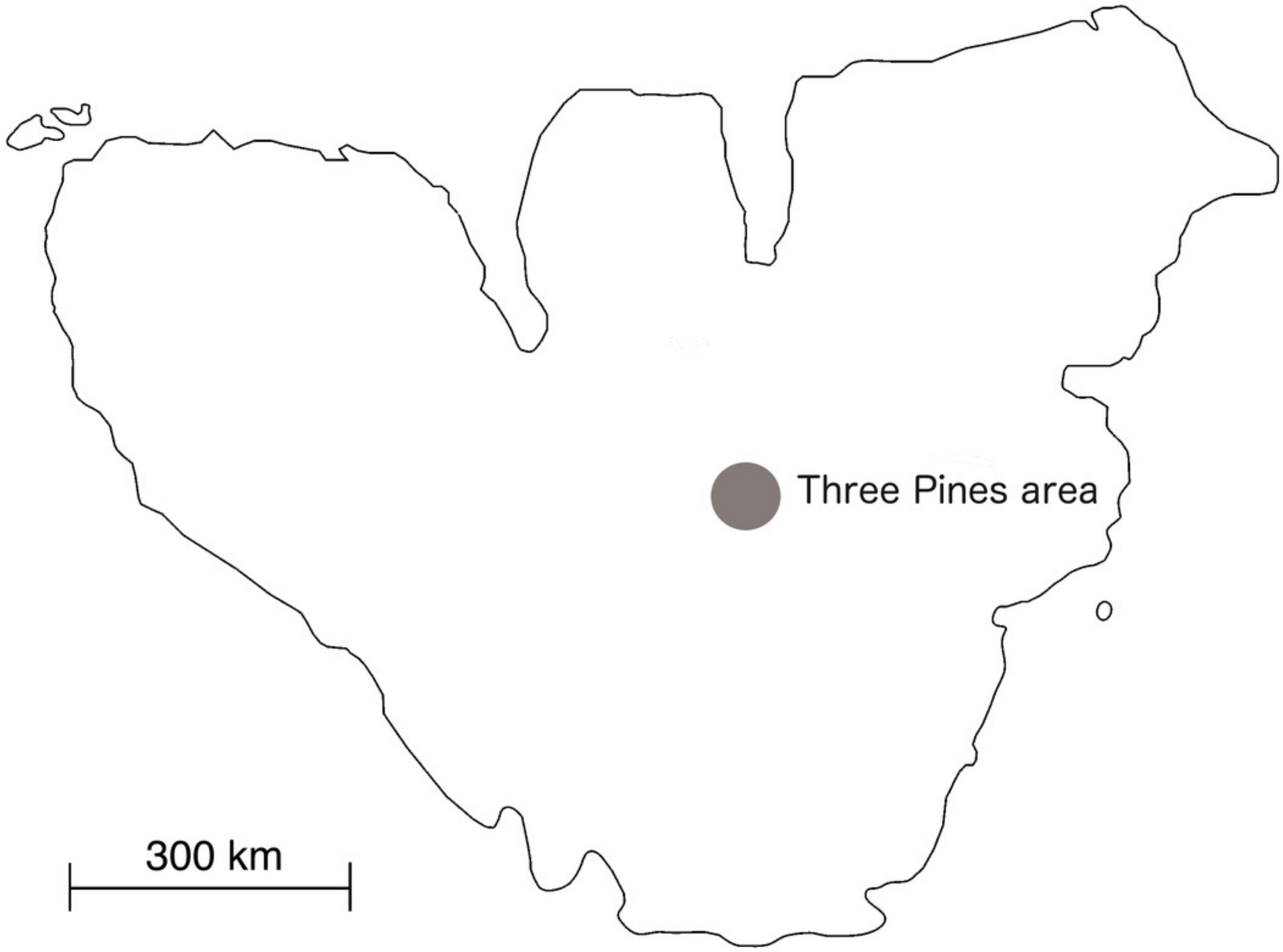

Table 1(on next page)

Whirling trial results, in summary.

Pholcid survivorship after 48 hours was recorded as Y (survived) or N (died). Whirling duration was recorded in seconds, or as N if no whirling was observed.

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2666v1 | CC BY 4.0 Open Access | rec: 21 Dec 2016, publ: 21 Dec 2016

Predator	Trial	Survivorship	Whirling Obs.	Mean Duration (s)	Total Duration (s)
T. ensifera	1	Y	1	20	20
	2	Y	0	0	0
	3	Y	0	0	0
	4	Y	0	0	0
	5	N	0	0	0
	6	Y	0	0	0
	7	Y	0	0	0
	8	N	0	0	0
	9	Y	0	0	0
	10	Y	0	0	0
L. noctua	1	Y	0	0	0
	2	N	0	0	0
	3	N	1	10	10
	4	Y	0	0	0
	5	Y	0	0	0
	6	Y	0	0	0
	7	Y	0	0	0
	8	Y	1	900	900
	9	Y	0	0	0
	10	Y	0	0	0
A. rufipes	1	Y	1	30	30
	2	N	0	0	0
	3	Y	1	10	10
	4	Y	1	15	15
	5	Y	3	903.75	3600
	6	Y	0	0	0
	7	Y	0	0	0
	8	Y	1	30	30
	9	Y	0	0	0
	10	Y	1	600	600

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2666v1 | CC BY 4.0 Open Access | rec: 21 Dec 2016, publ: 21 Dec 2016

Table 2(on next page)

Full observations.

The observations lasted five minutes, therefore the maximum recorded whirling duration is 300s. Any trial in which the pholcid was still whirling at the end of the five-minute observation window prompted longer observation. Whirling lasting longer than 300 seconds was recorded as “300s ([full duration]).”

		Day 1					Day 2						
Predator	Trial	Obs. 1	2	3	4	5	1	2	3	4	5	Mean/Total Duration (s)	# Whirls
T. ensifera	1	N	N	N	N	N	20s	N	N	N	N	20/20	1
	2	N	N	N	N	N	N	N	N	N	N	0/0	0
	3	N	N	N	N	N	N	N	N	N	N	0/0	0
	4	N	N	N	N	N	N	N	N	N	N	0/0	0
	5	N	N	N	N	N	N	N	N	N	N	0/0	0
	6	N	N	N	N	N	N	N	N	N	N	0/0	0
	7	N	N	N	N	N	N	N	N	N	N	0/0	0
	8	N	N	N	N	N	N	N	N	N	N	0/0	0
	9	N	N	N	N	N	N	N	N	N	N	0/0	0
	10	N	N	N	N	N	N	N	N	N	N	0/0	0
L. noctua	1	N	N	N	N	N	N	N	N	N	N	0/0	0
	2	N	N	N	N	N	N	N	N	N	N	0/0	0
	3	N	N	N	N	N	10s	N	N	N	N	10/10	1
	4	N	N	N	N	N	N	N	N	N	N	0/0	0
	5	N	N	N	N	N	N	N	N	N	N	0/0	0
	6	N	N	N	N	N	N	N	N	N	N	0/0	0
	7	N	N	N	N	N	N	N	N	N	N	0/0	0
	8	N	N	N	N	N	N	N	N	N	300s (900s)	900/900	1
	9	N	N	N	N	N	N	N	N	N	N	0/0	0
	10	N	N	N	N	N	N	N	N	N	N	0/0	0
A. rufipes	1	30s	N	N	N	N	N	N	N	N	N	30/30	1
	2	N	N	N	N	N	N	N	N	N	N	0/0	0
	3	N	10s	N	N	N	N	N	N	N	N	10/10	1
	4	N	N	N	15s	N	N	N	N	N	N	15/15	1
	5	5s, 5s	N	300s (3600s)	-*	N	N	N	N	N	N	903.75/3610	3
	6	N	N	N	N	N	N	N	N	N	N	0/0	0
	7	N	N	N	N	N	N	N	N	N	N	0/0	0
	8	N	N	N	N	30s	N	N	N	N	N	30/30	1
	9	N	N	N	N	N	N	N	N	N	N	0/0	0
	10	N	N	N	N	N	300s (600s)	N	N	N	N	600/600	1

*denotes a continuation from the previous observational window

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2666v1 | CC BY 4.0 Open Access | rec: 21 Dec 2016, publ: 21 Dec 2016