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SIZE AND MOTHERHOOD OF THE SPIDER *PHOLCUS ANCORALIS* (ARANEAE: PHOLCIDAE) AFFECTS WHIRLING AND OTHER DEFENSIVE BEHAVIORS

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Abstract. Defensive animal behavior is often a tradeoff between the energetic costs of defense and predator avoidance, with most animals choosing actions with the lowest energetic expense to evade their predators. *Pholcus ancoralis* is an introduced spider to Mo'orea, French Polynesia. I studied its defensive behaviors, with an emphasis on whirling, an energetically costly behavior which involves continual gyrations of the body. Different instars as well as females carrying egg sacs were disturbed with tactile, vibratory, and air movement stimuli to determine if larger instars and females with eggs have a higher whirling duration and frequency of defensive behaviors. *P. ancoralis* also faced the potential spider predators *Thorelliola ensifera* (Salticidae), *Tangaroa tahitiensis* (Uloboridae), and *Leucauge granulata* (Tetragnathidae) in a laboratory setting to determine if a higher whirling duration and higher frequency of defensive behaviors would lead to increased survivorship. The tactile stimulus elicited the greatest frequency and duration of whirling from *P. ancoralis*. Adult pholcids had the highest whirling frequency and duration out of all the instars, with egg-carrying females displaying an even greater response than other adults. Third and younger instars chose to retreat significantly more than adults, suggesting a change in defensive strategies during development. Whirling was not associated with a higher survivorship of *P. ancoralis* in the presence of potential predators, although repelling the predator and dropping away from it was. Thus, whirling is not an appropriate response to *T. ensifera* because it is conspicuous, energetically expensive, and does not promote survivorship. The inefficacy of whirling in this study suggests that this behavior may have arisen to defend against other salticids or other native natural enemies which *P. ancoralis* escaped upon its introduction to Mo'orea.

Key words: *cellar spider, costs, daddy-long-legs, energetics, French Polynesia*

INTRODUCTION

Defensive animal behavior is commonly a tradeoff between energetic costs and avoiding predation (Lima 1998). The majority of prey animals cease conspicuous, high-energy activities in favor of behaviors like hiding and remaining motionless when they detect their predators (Lima and Dill 1990). The costs and benefits associated with utilizing cryptic defense mechanisms are readily apparent;

motionless prey may be less apparent to predators, but the time spent hiding represents a loss in time spent foraging and eating. Animals which exhibit increased activity as a defensive strategy are few, such as the rapid spiraling of the zooplankton *Bosmina longirostris* to its copepod predator (Li and Li, 1979). The decision to reduce the level of normal foraging activities in favor of defensive action, which may lead to decreased food intake, can take a significant toll on an

organism. This may result in delayed maturity, smaller body size, and decreased fecundity (Lima and Dill 1990, Jakob 1991, Skow and Jakob 2003). So given these costs, why do active defensive strategies exist?

Little research has been done on the Pholcidae family, which consists of haplogyne spiders known colloquially as “daddy-long-legs” (Huber 2000, Eberhard and Briceno 1983). The pholcid *Pholcus phalangioides* performs an unusual behavior dubbed “whirling” when it is disturbed (Murphy 1914, Jackson et al. 1990, Jackson 1990, Heuts et al. 2001). Whirling consists of a pholcid spinning its body in flat, circular motions (Heuts et al. 2001). At high speeds, this can cause the pholcid to appear as an indistinguishable blur to humans. The exact purpose of this defense mechanism is not known, although an anti-predator function seems most likely (Jackson et al. 1990, Heuts et al. 2001). Heuts et al. (2001) proposed that it may be responsible for disturbing sensimotor processes in the visually acute Salticidae family of jumping spiders, some of which are predators of pholcids (Su et al. 2007). One study documented *P. phalangioides* exhibiting long-duration whirling, defined as low-speed whirling typically lasting two hours or more; this was said to occur specifically in response to araneophagic salticids as opposed to other arachnids (Heuts et al. 2001).

Pholcus ancoralis (Koch, 1865) is a pholcid found across Micronesia and Polynesia, which builds sheet webs on dense vegetation in damp, shady habitats (Beatty et al. 2008, Marples 1955). In Mo’orea, French Polynesia, it is commonly found on the buttresses of *Inocarpus fagifer* (Tahitian chestnut) and various ferns in the heavily canopied *I. fagifer*-dominated forests (Berland 1942, Yang 2008). Very little is known about this species, although it is likely a native to Samoa (Beatty et al. 2008, McCormack 2007) and is known to facultatively live in groups on sheet webs (Ochomogo 2002). Like *P. phalangioides*, *P. ancoralis* exhibits whirling behavior when disturbed.

The purpose of this study was to examine factors which may lead to differences in the defensive behaviors exhibited by *P. ancoralis* in response to tactile, vibratory, and air movement stimuli as well as potential predators. I was particularly interested in whirling behavior and its efficacy in promoting survivorship, given the relatively high energetic investment that whirling likely represents to both juveniles and adults, especially females carrying egg sacs. Previous studies have been performed on the whirling of *P. phalangioides* in response to various stimuli (Jackson et al. 1990, Murphy 1914); however, no studies have compared responses across all of the instars as well as compared maternal defensive responses to normal adult responses. Differences in whirling and other defensive behaviors will have implications on energetic tradeoffs inherent in costly defensive strategies. I predicted *P. ancoralis* would whirl and react with the greatest frequency and duration to the tactile stimulus, which most resembles a physical attack by a predator. I hypothesized that air movement would elicit the least response, as it resembles gusts of wind which frequently disturb the webs, and that vibratory stimuli would elicit a medium frequency of defensive behaviors.

Past studies have suggested that predators have a lower predation rate on larger-sized prey as well as those of a greater larval instar, because these prey have more antipredator defenses and there is a greater risk and handling time associated with pursuing them (Whitman and Vincent 2008, Ramirez et al. 2010, McClure and Despland 2011). I predicted a trend in which larger instars would whirl longer and exhibit more defensive behaviors than smaller instars, culminating in adult *P. ancoralis* spiders whirling the longest and displaying the greatest frequency of other behaviors in response to the experimental stimuli. I also hypothesized that adults would have the highest survivorship when experimentally placed with potential predators.

Female pholcids carry egg sacs about the size of their abdomens in their jaws, so defensive actions like whirling and running from predators likely represent greater energetic costs to them compared to remaining motionless. Therefore, female pholcids carrying egg sacs were expected to have the highest frequency of whirling, given their relatively vulnerable state, but not necessarily the longest duration, due to fatigue associated with gyrating with a heavy burden.

Finally, I was interested in determining whether long-duration whirling would be present in *P. ancoralis*, since Heuts et al. (2001) suggested it is an exclusive response which *Pholcus phalangioides* displays towards araneophagic jumping spiders (Salticidae). I predicted that long-duration whirling would be present in *Pholcus ancoralis* as an exclusive response to *Thorelliola ensifera*, a salticid which was considered a potential predator of the pholcid in this study. A higher frequency and duration of whirling was expected to correlate with a higher survivorship of *Pholcus ancoralis* individuals when experimentally placed with salticid predators.

METHODS

Study site

This study was conducted in Mo'orea, French Polynesia, in the *Inocarpus fagifer*-dominated forest on which the Three Pines Trail (17°32'23.55"S, 149°49'33.08"W) is located. This forest is characterized by high canopy cover, medium litter layers, and ferns as the dominant cover plant. The *Inocarpus fagifer* trees generally had litter and large boulders in their vicinity, leaving a clear space between the buttresses for *Pholcus ancoralis* and other spiders to build their webs.

Selection of study organisms

Pholcus ancoralis living on *Inocarpus fagifer* trees were selected at least 10m away from the

trail to ensure that human disturbance would not affect their behavior. Although they also occur on other low-lying vegetation, pholcid populations were selected exclusively from *I. fagifer* buttresses to control for confounding factors related to a difference in habitats. The spiders were selected haphazardly to obtain equal numbers of variously sized pholcids as well as egg-carrying females.

Potential predators

Spiders from the Salticidae, Uloboridae, and Tetragnathidae families were chosen as potential predators of *Pholcus ancoralis* because all three are commonly found in the *I. fagifer* forest. *Thorelliola ensifera* (Thorell, 1887), an introduced salticid with a body length of 5 mm, is commonly found on the leaves of broad-leafed cover plants as well as the trunks of *I. fagifer*, often in close proximity to *P. ancoralis* webs (McCormack 2007). *Tangaroa tahitiensis* (Berland, 1934) is a polymorphic, native uloborid which builds orb webs on exposed vegetation as well as below *P. ancoralis*' webs on *I. fagifer* buttresses (Gillespie et al. 2002). *Leucauge granulata* (Walckenaer, 1842) is a native tetragnathid with an orange cephalothorax and black legs which is also found building orb webs on exposed, low-lying vegetation (Gillespie et al. 2002).

T. tahitiensis and *L. granulata* were used as control predators, because they were not expected to actively hunt *P. ancoralis* and I wanted to note any defensive behaviors that *P. ancoralis* might exhibit to non-salticid heterospecifics.

Responses to artificial stimuli

I conducted observations to determine what defensive behaviors *P. ancoralis* displays in a similar manner to artificial stimuli. The three cues were tactile, vibratory, and air movement. I presented an artificial stimulus to a motionless focal individual, and noted how long it whirled and any other behaviors it showed. I gave the pholcid a minute to rest

TABLE 1. Size classes of *P. ancoralis* and the corresponding instars. 5th instars can either be mature or penultimate juveniles depending on their nutritional state during development.

Size Class	Abbreviation	Instar	Juvenile vs. Adult
Extra small	XS	1 ST – 2 ND	Juvenile
Small	S	3 RD	Juvenile
Medium	M	4 TH	Juvenile
Large	L	5 TH	Juvenile or Adult*
Extra large	XL	6 TH	Adult

after it had ceased whirling before provoking it with the same stimulus again, to obtain a replicate response for each individual. Replicates were not possible for individuals which ran or dropped out of sight.

I prodded individuals (n=200) with the tip of a pen, usually striking their legs. I simulated air movement by puffing air out of a turkey baster 5 cm from the spiders (n=228). The puff of air usually came from above the spider, which was the most convenient direction to point the tip of the turkey baster without disturbing the web. I used vibrating forceps as a vibratory stimulus, and placed the tips of it on a section of the web 5 cm from the focal individuals (n=181).

Factors affecting survivorship of pholcids from potential predators

I conducted experiments in a laboratory at the Richard B. Gump Field Station to test the efficacy of defensive behaviors and other factors affecting survivorship of *Pholcus ancoralis* to potential predators found in the field (n=131). I used different-sized pholcids, ranging from extra-small (XS) to extra-large (XL). These size classes corresponded to different instars of *P. ancoralis*, with L pholcids representing either adults or penultimate juveniles (Table 1); poorly fed pholcids may need 6 molts to reach maturity, although they attain sizes significantly larger than those that mature at 5 molts (Jakob and Dingle 1990).

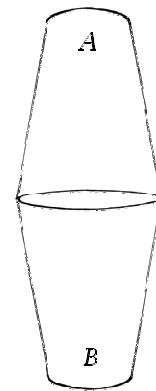


FIG. 1. The survivorship trials took place in a chamber comprised of two 150 mL cups. *P. ancoralis* generally preferred the top of the chamber at position A, and potential predators were initially placed at the opposite end of the chamber at position B.

I placed one pholcid into a chamber and allowed it to acclimatize to its surroundings for at least 20 minutes before I introduced a potential predator at the opposite end of the chamber (Fig. 1). Potential predators were not given time to become accustomed to the cup before having contact with the pholcid in order to simulate situations where they might invade *P. ancoralis'* web.

I observed the two spiders for up to an hour, in which whirling duration, frequencies of other defensive behaviors, and survivorship of *P. ancoralis* was noted. Pholcids which had

TABLE 2. Ethogram of defensive behaviors

Behavior	
Attacking	Rapidly approaching followed by wrapping the stimulus/ individual
Dropping	Dropping at least 5 cm from the web in height
Retreating	Moving from the web to the tree trunk and remaining motionless
No Response	A lack of response to the stimulus/individual as determined by a lack of movement
Repelling	Using the legs to push away a stimulus/individual
Rocking	Horizontal swaying of the body
Running	Moving at least 5 cm away at a rapid speed from the stimulus/individual
Whirling	Swinging the body in circles whilst upside down with tarsi on the web
Short-duration Whirling	Whirling which lasts less than 30 min, generally between 5-120s
Long-duration whirling	Whirling which lasts more than 30 min. generally at least 2 hrs

survived the hour were given an additional 23 hours with the predators and their survivorship was checked one last time before the trial ended 24 hours after initial contact. Trials also ended once the predator launched a successful attack on the pholcid, resulting in the individual in the spider's jaws. The same was true when the pholcid killed the unsuccessful predator and wrapped it in silk.

Statistical analysis

I performed a one-way ANOVA to look at differences in whirling times in response to different stimuli, potential predators, and size classes. After the ANOVA tests, Tukey-Kramer tests distinguished the stimuli or size classes which had significantly different responses. Pearson's Chi-squared tests were performed to determine the differences in defensive response types among different size classes, as well as between egg-carrying females and other adults. I also performed Chi-squared tests in order to see if a particular defensive behavior led to a higher survivorship of pholcids. Additionally, it

assessed differences in potential predator mortality between females with eggs and other adult pholcids. I calculated a t-test statistic in order to test whether whirling duration would lead to higher survivorship of pholcids at 1 and 24 hours. I did a logistic regression to determine whether survivorship at 1 and 24 hours depended on the frequency of a certain response. Statistical analyses were run on JMP 9.0 (JMP) and P-values less than or equal to 0.05 were considered significant.

RESULTS

Responses to artificial stimuli

P. ancoralis displayed different behavioral responses to tactile, vibratory, and air movement stimuli in experiments conducted in the field (Table 2). The frequency and duration of whirling was different among these stimuli (One-way ANOVA, $F_{2, 1178} = 41.40$, $P < .0001$), with the tactile stimulus garnering a significantly different response from the vibratory and air movement stimuli (Tukey-Kramer Test, $P < .0001$) (Fig.2). *P. ancoralis*

TABLE 3. Frequencies of behavioral responses expressed in percentage to each of the three artificial stimuli. Behaviors which made up the majority of responses for each stimuli are bolded.

Stimulus	Whirl	Run	Drop	Attack	Rock	Retreat	No Response
Tactile	53%	13%	11%	0%	8%	8%	7%
Air Movement	22%	23%	4%	0%	7%	7%	30%
Vibratory	8%	4%	0%	53%	3%	3%	31%

whirled in 67% of all observations when prodded compared to only 20% when blown with a gust of air or 8% when vibrated on the web. There was no difference in the whirling response between the air movement and vibratory stimuli (Tukey-Kramer Test, $P = 0.99$).

Defensive behaviors besides whirling also varied according to the artificial stimuli presented to *P. ancoralis* (Table 3). The spiders sometimes exhibited more than one behavior in response to a stimulus; for example, some chose to both run and drop in order to escape the perceived danger. Rocking was a common transitional behavior as the pholcids slowed from whirling to a stop. Vibrating the web with forceps caused pholcids to rapidly approach the source 20% of the time, and attempt to wrap it 33% of the time, making up 53% of all defensive behaviors observed in the vibratory stimulus trials. There was also a significant difference seen in spiders which did not respond to the cues (Pearson's Chi-Squared Test, $X^2=62.249$, $dF=2$, $P < .0001$).

Spiders exposed to an air movement or vibratory stimulus exhibited no response more often than those exposed to a tactile stimulus (Tukey-Kramer Test, $P < .0001$).

Responses by spider size to artificial stimuli

The different sizes of *P. ancoralis* exhibited significantly different whirling responses and other defensive behaviors (One-way ANOVA,

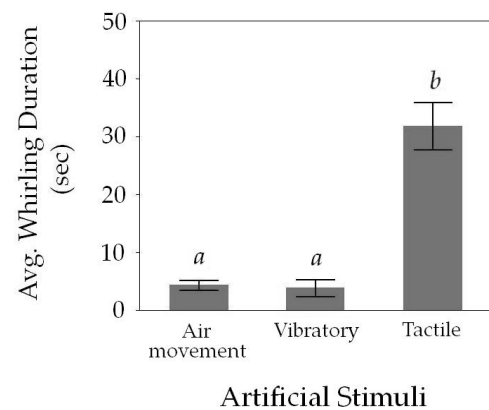


FIG. 2. A comparison of the average whirling durations with respective standard deviations in response to the three artificial stimuli (One-way ANOVA, $F_2=41.40$, $P < .0001$). The error bars represent a standard deviation from each mean. Different letters represent stimuli which are different from each other.

$F_4=8.22$, $P < .0001$). Larger spiders exhibited both greater whirling duration and higher whirling frequency among individuals (Fig. 3). Correspondingly, the XL or adult spiders showed the greatest difference in response to XS and S spiders (Tukey-Kramer Test, $P < .0001$). While there was no difference in running, dropping, or rocking frequencies between all the sizes, larger spiders were more likely to attack a vibrating source than smaller ones. XS and S spiders were more likely to retreat against the tree trunk than XL spiders, as indicated by the significant difference seen

in this behavior among the size classes (Pearson's Chi-Squared Test, $X^2 = 23.80$, $dF=4$, $P < .0001$). XS spiders were also more likely to fail to respond to the cues than XL spiders, which were generally more reactive.

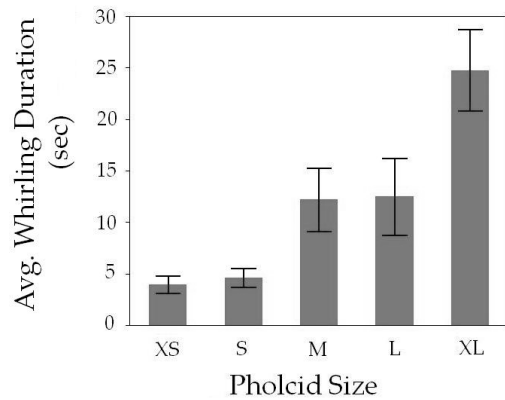


FIG. 3. Comparisons of average whirling duration for each size class of pholcids. XL spiders had a significantly higher whirling time compared to XS and S spiders (Tukey-Kramer Test, $P < .0001$), whose responses were nearly identical; the same was true when comparing M and L pholcids (Tukey-Kramer Test, $P = 0.999$; Tukey-Kramer Test, $P = 1.000$). The error bars represent one standard deviation from the mean.

Maternal responses to artificial stimuli

P. ancoralis carrying eggs differed from other XL spiders in nearly all of the behavioral responses. Females with eggs were significantly more likely to whirl, with 48% whirling compared to 16% in the same-sized pholcids. (Pearson's Chi-Squared Test, $X^2 = 12.72$, $dF=1$, $P = .0004$). Their whirling duration was significantly different than pholcids without eggs, with a mean whirling time of 49s compared to the 3 s average of other XL pholcids (t-test, $t_{206} = 4.66$, $P < .0001$). Females carrying egg sacs were also found to be more likely to run, rock, and retreat (Pearson's Chi-Squared Test, $X^2 = 9.12$, $dF=1$, $P = .0025$; Pearson's Chi-Squared Test, $X^2 = 8.48$,

$dF=1$, $P = .014$; Pearson's Chi-Squared Test, $X^2 = 3.938$, $dF=1$, $P = .05$). However, they were less likely to approach and attempt to wrap a vibrating source on their web (Pearson's Chi-Squared Test, $X^2 = 39.44$, $dF=2$, $P < .0001$).

Factors affecting survivorship of pholcids exposed to potential predators

Higher whirling duration did not affect survivorship of pholcids at 1 or 24 hours when placed with potentially araneophagic predators (t-test, $t_{128} = 0.21$, $P = 0.83$). Behaviors such as running and rocking similarly did not play a role in whether or not a pholcid would survive the 24 hour-long trial. The attacking behavior of approaching and attempting to wrap a predator was rarely seen during the first hour of the trial, although wrapped predators were observed in 28% of the completed trials. Behaviors like dropping from the top of the chamber as well as repelling and flinching away from the predator made a difference in the survivorship of pholcids during the first hour of contact with another spider species (Logistic Regression, $X^2 = 8.12$, $dF=1$, $P = .0044$; Logistic Regression, $X^2 = 15.86$, $dF=1$, $P < .0001$; Logistic Regression; $X^2 = 13.45$, $dF=1$, $P = .0002$). Higher instances of these behaviors correlated with greater survivorship. However, the instances of flinching observed in the first hour did not make a difference in overall survivorship at 24 hours, unlike repelling and dropping (Logistic Regression, $X^2 = 2.52$, $dF=1$, $P = 0.11$; Logistic Regression, $X^2 = 4.64$, $dF=1$, $P = .03$; Logistic Regression, $X^2 = 11.4$, $dF=1$, $P = 0.008$).

Size played an important role in survivorship, with a clear trend showing larger spiders with greater survivorship rates (Fig.4). In fact, there were no instances of predation-induced mortality among the L and XL size classes of *P. ancoralis* in the 131 laboratory trials.

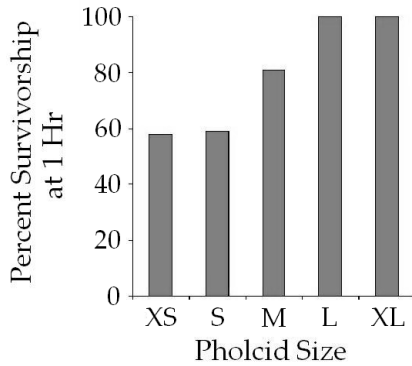


FIG. 4. Comparisons of survivorship at 1 hr between five size classes of pholcids indicating a trend of greater survivorship in larger spiders (Pearson's Chi-Squared Test, $X^2=27.22$, $dF=4$, $P < .0001$)

Survivorship to potential predators

There was a marked difference in survivorship of pholcids when placed with the salticid *T. ensifera* compared to the non-salticids, *L. granulata* and *T. tahitiensis* (Pearson's Chi-Squared Test, $X^2=11.31$, $dF=2$, $P = 0.0035$) (Table 4). *T. ensifera* was the only spider which ever displayed an interest and actively hunted *P. ancoralis*, whereas *L. granulata* and *T. tahitiensis* generally chose to build webs in the bottom half of the chamber, since *P. ancoralis* almost always occupied the ceiling.

Responses of females carrying eggs

Females with egg sacs did not display significantly different defensive behaviors in the lab when confronted with other spiders. They neither whirled more frequently nor longer than other XL spiders in response to *L. granulata*, *T. tahitiensis*, and *T. ensifera*. Like all other L and XL pholcids, all of the females carrying egg sacs survived the entirety of the 24 hour trial. One notable difference was a significantly lower rate of predator spider mortality associated with the females carrying eggs compared to same-sized conspecifics (Pearson's Chi-Squared Test, $X^2=5.38$, $P = .02$). Females carrying egg sacs killed and wrapped

TABLE 4. Percent survivorship of *P. ancoralis* after 1 and 24 hours of exposure with potential predators.

Predator	1 Hour	24 Hours
<i>L. granulata</i>	100%	88%
<i>T. tahitiensis</i>	100%	100%
<i>T. ensifera</i>	74%	61%

potential predators in 31% of trials compared to 71% in non-mother, XL-sized pholcids.

Long duration whirling

Long duration whirling was an extremely rare behavior of *P. ancoralis* in both the *Inocarpus fagiger* forest and the laboratory setting. I observed this behavior in a natural setting only once during the collection of preliminary data; it was performed by a medium-sized, four-legged, individual in response to the tactile stimulus and lasted for 59 minutes. This instance in the field stands alone out of 1,476 observations with the 3 artificial stimuli. Two instances of long duration whirling by medium-sized pholcids occurred out of 130 laboratory trials; these lasted over two and four hours respectively.

DISCUSSION

Responses to artificial stimuli

In this study, I exposed *Pholcus ancoralis* to three different stimuli to determine whether it would exhibit a different defensive response to one stimulus. While the exact function of whirling has never been proven, previous investigators including this one assume that an anti-predator purpose is the most applicable, as I tested in the trials with potential predators (Jackson et al. 1990, Jackson et al. 1992, Heuts et al. 2001).

Out of the three stimuli, the tactile stimulus most resembles an attack by a

predator or confrontation by a conspecific. *P. ancoralis* therefore had a higher whirling response to being prodded compared to being blown or vibrated; Jackson et al. (1990) similarly reported that pholcids are more likely to whirl to tactile and mechanical stimuli than air movement ones. Whirling is relatively energetically costly because it involves propelling the hanging spider's body in circles from a single attachment point on web. It generally continues much longer than any other behaviors observed, with an average of 32 seconds to the tactile stimulus. Even though whirling was the most energetically expensive behavior observed, it was more common than evasive behaviors to the tactile stimulus. This suggests that *P. ancoralis* is willing to exert more energy to defend against physical attacks.

Blowing air at the pholcids induced the most variable set of responses, with evasive behaviors (running, dropping, retreating) making up 41% of the total response. Because most of the air movement that they experience probably comes in the form of wind, evasive behaviors such as retreating from the exposed web to the tree trunk would protect them from being blown away. Since most web-disturbing gusts are relatively gentle and brief, pholcids could also save energy by not reacting at all, which occurred in 30% of the observations.

Vibration of the web mostly elicited either no reaction or attacks on the vibrating source. The vibrations felt by the pholcids seem to resemble prey landing on their webs; this may explain why they attack more than whirl to it.

Rocking was often seen as a transitional behavior between whirling and immobility, sometimes manifesting after the spider had been whirling for longer than a minute. *P. ancoralis* was observed to transition from whirling to rocking and then back to whirling in observations which lasted several minutes. Maintaining a rocking motion requires a smaller change in initial input of energy when the spider switches back to whirling than it would if it had to start from complete rest again. Rocking may also allow the spider to

slow down since coming to an abrupt halt from gyrating its body for minutes at a time might have adverse effects on its physiology; eggs may be especially vulnerable to centripetal forces and detach from the egg sac otherwise. While rocking is linked to whirling, it did occur on its own in some cases, and its function seems to be more transitional than defensive in nature.

Responses by spider size

Adult, or XL pholcids, were observed to whirl more often and for a longer time. *P. ancoralis* often lives in groups and larger spiders tend to win intraspecific competition for prey landing in webs (Jakob 1991), so adults generally consume more than juveniles and correspondingly, have more energy to expend. Adult spiders may also represent the survivors of various predator attacks, and be more reactive due to their experiences. It is also possible that due to their large size, adults are greater targets than the smaller instars for predation by vertebrate predators (Whitman and Vincent 2008). Jackson et al. (1990) hypothesized that whirling may cause pholcids to look larger and more intimidating to predators, and this can deter non-salticid predators. Therefore, whirling is a more important defensive strategy for larger, more conspicuous pholcids to utilize than smaller spiderlings when stimulated with a physical cue.

Retreating was a behavior more common to the XS and S spiders, suggesting a change in defensive strategies with size, and thereby with age. Since the smaller instars appear transparent gray in color, they are more camouflaged than adults when motionless on a tree trunk. Retreating is an ideal strategy for small *P. ancoralis* spiders because it does not require as much energy as whirling. It seems effective for smaller, cryptic spiders since they are unlikely to run fast enough from a predator. Longer legs aid defense, because predators are more likely to contact the legs than the body of this spider (Jackson et al.

1990). With shorter and weaker legs, smaller spiderlings have fewer defenses than adult *P. ancoralis* and should avoid confrontations with predators.

Spiders that were M and L-sized whirled less often than adult XL spiders, but more often than S and XS spiders. While they are large enough to be seen by vertebrate predators, they are not as perceptible as adult spiders. These spiders are also unlikely to match XL spiders in prey consumed, so their lower whirling duration may be a reflection of this difference in energy consumption.

Responses of females carrying eggs

Females carrying eggs had a greater whirling and overall defensive response than other XL pholcids, likely because of their increased vulnerability and protective maternal responses. The light gray color of the 2-3mm long egg sacs, which they carry in their jaws, makes them more conspicuous against the dark corners of the buttresses that they build their webs on. Salticids are well known for their abilities to distinguish colors and discriminate between prey based on visual cues (Jakob et al. 2007, Jackson 2010), so they may find females carrying egg sacs more apparent than other pholcids. Females carrying egg sacs may try to mitigate the vulnerability associated with carrying a large, conspicuous load by employing more defensive behaviors, as seen in their tendency to run, rock, and retreat more often. There has been previous documentation in other spiders of egg guarding (Horel and Gundermann 1992) and protecting young from predators (Fink 1986, Fink 1987, Schneider and Lubin 1997), and the differences in defensive responses between reproductive females and other adults suggests that *P. ancoralis* also exhibits protective maternal responses to perceived threats.

Reproductive females had a lower attack rate to the vibratory stimulus than other adult pholcids, suggesting that they are less responsive to potential prey landing in webs.

Oftentimes, multiple spiders in the communal webs would respond to vibrations of the web; adult spiders especially seemed willing to travel up to 30cm to investigate vibrations occurring next to the focal individual. Females carrying egg sacs were never observed investigating sources of vibrations coming from another part of the web inhabited by other spiders. Thus, it appears that females carrying eggs consume less prey to begin with, yet they expend much more energy when engaging in defensive behaviors. Since holding their egg sacs may be crucial for egg survival, the possibility of an increase in fitness associated with maternal care appears to be worth the tradeoff of a higher energetic consumption relating to whirling whilst egg guarding (Fink 1986).

Efficacy of defensive behaviors

I tested the efficacy of *P. ancoralis*' defensive behaviors by placing it in a chamber with potential predators and noting which behaviors were correlated with individuals which had survived the 24 hour trial. *L. granulata* and *T. tahitiensis* did not interact with *P. ancoralis* nor did they elicit more than an occasional response, so I will only be treating *T. ensifera* as a predator.

Greater whirling duration unexpectedly did not lead to greater survivorship in *P. ancoralis* when it encountered *T. ensifera*. The lack of a web in the chamber may explain the loss of whirling efficacy, as Jackson et al. (1990) suggested that pholcids must be able to detect potential predators in order to whirl effectively or they were more likely to get captured. However, *T. ensifera* was observed attacking *P. ancoralis* mid-whirl, implying that whirling is not effective in disturbing the salticid's sensimotor processes; in fact, in cases where the pholcid was whirling at very slow speeds, it may have attracted the salticid's attention to the pholcid (Dill 1975), thereby lowering its chances of survival.

Whirling behavior may have evolved to protect against predators other than salticids.

P. ancoralis is an introduced species from Samoa (McCormack 2007), and whirling may be effective against native Samoan predators. Other studies have shown that excessive motion like vigorous thrashing, rolling, head flicking, and jumping can allow insects to evade parasitoids (Gross 1993); whirling may be another evasive behavior for parasites and egg parasitoids, which can also explain why females with eggs are more likely to whirl. As an introduced species to Mo'orea, *P. ancoralis* may have escaped any natural enemies which the whirling mechanism was evolved for, since introduced populations tend to be less parasitized due to a lower probability of transporting their parasites with them to new locations (Torchin et al. 2003).

Repelling and dropping were useful strategies for avoiding predation, while flinching did not lead to increased survivorship in completed 24 hour trials. Repelling predators away with their long legs was effective in driving them away, because the force of the push would cause the potential predator to drop from the top of the chamber, where the pholcid usually rested, to the bottom. The positive correlation between the frequency of repelling and the size of the pholcid may explain the success of larger spiders in avoiding predation. Dropping was effective because it immediately removed the pholcid from the potential predator's vicinity.

Long Duration Whirling

Long duration whirling was a very rare occurrence throughout the course of this study. I observed it a total of four times out of approximately 1,600 observations in the field and laboratory. Although Heuts et al. (2001) reported the presence of long duration whirling in *Pholcus phalangioides* in response to six out of eight salticid species, long duration whirling does not appear to be a common response by *Pholcus ancoralis* to the salticid *Thorelliola ensifera*.

Conclusion

Although whirling as a possible defense mechanism in pholcids has been studied in detail in *Pholcus phalangioides* (Jackson et al. 1990, Jackson 1990, Heuts et al. 2001), this study is the first to document the defensive responses of *Pholcus ancoralis* and their efficacy in aiding survival when individuals are exposed to potential predators. I found that this spider changes its defensive strategies during its development, since smaller instars chose less costly behaviors than adult pholcids. Egg-carrying females displayed differences in behaviors from other adults, suggesting that female *Pholcus ancoralis* actively protect their unborn young; this high cost in maternal care is likely mitigated by a possible increase in fitness associated with more offspring hatching. Whirling was shown to be an inappropriate defense to the salticid *Thorelliola ensifera* in this case, since it was conspicuous, expensive, and did not promote survivorship. *Pholcus ancoralis* may have escaped natural predators when it arrived on Mo'orea, but if its defensive strategies are not effective to predators there, then it may be experiencing trouble in paradise.

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