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THE INFLUENCE OF SIZE ON CANNIBALISM AND PREDATION IN HUNGRY WOLF SPIDERS (LYCOSIDAE, *HOGNA CRISPIPES*)

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Abstract. Size is an important factor that affects cannibalism in wolf spiders (Lycosidae). This study investigated the time for cannibalism to occur among pairs of different sized, hungry wolf spiders. In addition, the preference for smaller conspecific prey in the presence of larger alternative prey was examined. This study was the first to look at cannibalism in the wolf spider species found on Mo'orea, *Hogna crispipes*. Like other genera within the Lycosid family, which are known to have cannibalistic tendencies, *Hogna c.* spiders are capable of cannibalizing. Cannibalism occurred in 87.5% of the spider pairs. Of the spiders that did not cannibalize, a majority were of the same size. In addition, in the pairs of spiders that did cannibalize there was a strong negative relationship between the time for cannibalism to occur and the difference in size between pairs of spiders. This relationship followed a trend, where the spider pairs that were more similar in size generally took longer to cannibalize than the spider pairs that had larger size differences (≥ 3 mm). Lastly medium sized spiders did not have a predation preference for smaller conspecifics over larger alternative prey. This study provides a foundation about cannibalism in *H. crispipes*.

Key words: conspecific; prey preference; generalist predator; Surinam cockroaches; Mo'orea, French Polynesia

INTRODUCTION

Arthropod generalist predators, which are not limited to specific prey, can have both positive and negative effects on the ecology and composition of terrestrial arthropod communities. For example, generalist predators can be beneficial in agro ecosystems where they serve as natural biological control agents of harmful pests (Tolonen 1995). Non-specialized diet abilities become a problem however, in invasive species. Unlike specialized feeders, which are limited to habitats that are abundant in their specific prey, generalist feeders can be successful in exploiting new habitats where other arthropod populations become their new source of prey (Snyder 2006). Understanding the roles of arthropod generalist predators, whether favorable or detrimental, is important for the conservation or control of such organisms.

One example of important generalist predators are wolf spiders (Lycosidae). Like other valuable generalist predators, wolf spiders also serve as important biological control agents by preying on arthropod pests in agricultural crop fields. In addition to preying on other arthropods in the Insecta and Arachnida classes, wolf spiders are known to commonly predate on conspecifics, members of the same species (Hvam 2005, Nyffeler 1988). In the same manner that generalist predators are important in regulating other arthropod populations, cannibalistic predators play an important role in regulating their own populations (Buddle 2003).

Previous studies have primarily focused on species within the *Pardosa* genera. Studies demonstrated that cannibalism was more likely occur in pairs of hungry spiders and in pairs of largely different sized spiders. In addition, the time for cannibalism to occur

was shorter in pairs of hungry spiders in comparison to spiders that were not hungry (Petersen 2010, Samu 1999). Altogether, suggesting that both size and hunger are important factors influencing cannibalism.

This study investigates the role of predator-prey size differences in the cannibalistic and predatory behavior of the wolf spider species *Hogna crispipes*. The following hypotheses were tested: (1) Cannibalism will occur in all pairs of hungry spiders despite the size differences within pairs. (2) Cannibalism will take less time to occur in pairs of hungry spiders with larger size differences. (3) When given the choice of smaller conspecific spiders and larger Surinam cockroaches, *Pycnoscelus urinamensi*, medium sized, hungry spiders will have a preference for eating the smaller prey.

METHODS

Study species

Hogna crispipes (L. Koch 1877) McKay 1979 can be found in a range of habitats, coastal and inland, throughout Australia, New Zealand, and the Pacific Islands including the Society Islands (Dierkens 2011, Framenau 2006) *Hogna crispipes* are characteristic of sexual dimorphism, in which females have a larger abdomen in comparison to male spiders. Exterior physical features of these wolf spiders include brown or gray body colors and a pair of parallel dark stripes on the cephalothorax (Fig 1).

In addition to *H. crispipes*, Surinam cockroaches, *Pycnoscelus urinamensi* (Linnaeus 1758), which were found in the same habitat as the spiders, were used as alternative prey for one of the experiments.



FIG. 1. Male *H. crispipes* shown on left, female *H. crispipes* shown on right.

Study Site

On Mo'orea, French Polynesia, *Hogna crispipes* spiders were found on grass, dirt, and leaf litter substrates. Previous studies on cannibalism in wolf spiders have mostly focused on species within the *Pardosa* genera. Here, the wolf spider species *H. crispipes* was selected for this study.

H. crispipes were surveyed on four sites within the perimeter of the University of California Berkeley's Richard B. Gump South Pacific Research Station (17°29'26.49"S, 149°49'34.18"W) which is located along Cook's Bay on the island of Mo'orea, French Polynesia (Fig 2). Spiders and cockroaches were found in abundance on site 2. For this reason, site 2 was chosen as the site from which spiders and cockroaches were collected for experimental purposes. To measure for the density of actively hunting spiders, fifteen (2m x 3m) plots were set up to purposely cover different proportions of varying grass type substrates on site 2. A count of foraging spiders seen within each plot was recorded on this one time survey.

Preliminary studies took place beginning September 2012. Laboratory experiments from which data is presented in this study took place from October to November of 2012.

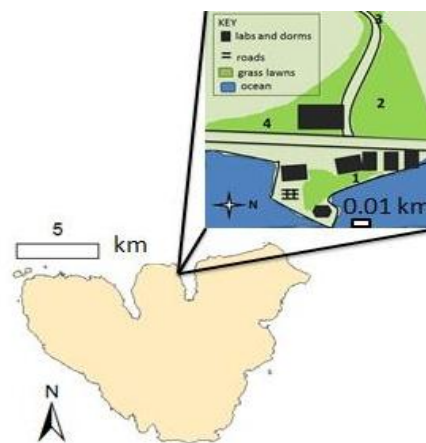


FIG. 2. Map featuring study sites on UC Berkeley GUMP Station in Mo'orea, French Polynesia (ArcMap 10.1)

Spider and cockroach collection

Using a headlamp, 6 spider collecting events took place on different dates during the night, when these spiders' eyes could be seen reflecting the light and the Surinam cockroaches could be easily found. All collected spiders and cockroaches were measured for body length, which I defined as the distance from the tip of the chelicera to end of the spinnerets for spiders and the distance from the tip of the head to the end of the thorax for cockroaches, before they were used for experimental purposes. Since most spiders weighed less than 1g, instead of mass, spider body length was used as a measurement for size. Spiders and cockroaches were housed individually in translucent glass vials (2.5 cm in diameter). A moist environment was kept for spiders and cockroaches by capping each vial with cotton that was wetted 2-3 times daily. All spiders were deprived of food for 5-6 days in order to ensure that they were similarly hungry. Spiders that were not used in this study include those that were less than 0.5 cm in size and female spiders that were found carrying an egg sac or carrying their newly hatched offspring.

Differences in spider size and cannibalism

Pairs of spiders with size differences of 0mm to 5mm were simultaneously placed in arenas. Arenas were made of plastic cups (6.7 cm diameter x 8.7 cm height) that were secured with screen mesh and rubber bands. Spiders from the same collecting events were paired up to ensure same starving conditions. A total of 80 spiders (40 pairs) that ranged from 0.5cm to 1.5cm in size were used in this experiment. The occurrence of cannibalism was observed among pairs during the first hour, and every 12 hours until cannibalism or death was observed in at least one spider. Spiders that cannibalized within minutes of the start of an experiment were given time values of 1 hr. I defined the occurrence of

cannibalism as the death of one spider from which only partial or no body remains were observed. Spiders that died of unknown causes, other than cannibalism, were those that were found with complete body remains and with their legs curled up.

To test for the relationship between the time for cannibalism to occur and the size difference between pairs of spiders, a Mechanistic Growth Fit Curve was applied to a "time for cannibalism vs. size difference" bivariate graph. A Linear Regression Analysis of the logarithmic (\log_{10}) function of "time for cannibalism vs. size difference," was performed.

Cannibalism and predation: prey size

Prey preference among conspecifics and alternative prey was examined. Field observations and preliminary data demonstrated that individuals of *H. crispipes* were capable of consuming Surinam cockroaches that were larger than them. For this reason, Surinam cockroaches were used as alternative prey in this experiment. Sixteen spiders were starved, measured, and kept as described previously. Eight cockroaches were caught one day previous to the experiment and were simultaneously placed with a medium (1.1-1.2 cm) spider and a smaller spider (0.6-0.7 cm) in individual arenas. Each group was set up so that there was a size difference of 5mm between the two spiders. In all cases, the cockroaches (1.7-1.8 cm) were 6mm larger than the medium sized spider. The chronological order in which a spider or cockroach was consumed was recorded. I defined preference for prey as the prey that was consumed first.

To test whether medium spiders had a preference for the smaller spiders over the larger cockroaches, a ChiSquare one-sample test for goodness of fit was used. All statistical tests were performed in JMP 10.

RESULTS

Field survey

Based on qualitative surveys from each site, spiders were more abundant on site 2 (Fig. 2), which was the largest of all sites (875 m²). On this site, spider density varied among 15 plots and ranged from 0 spiders per m² to 1 spider per m², with an overall average of 1 spider per 1/2 m² (standard error= 0.556). Similarly, in comparison to other lawns, more arthropods and other insects were seen on site 2. Spiders were seen foraging on the grass closer to midnight as opposed to earlier in the night. Throughout the time of the study (October-November 2012), foraging spiders, which ranged from 0.5cm to 1.5cm in body size, were observed on the grass substrate. Younger spiders (> 0.5mm) were usually found on their mother's backs or under rock and grass substrates. Females with egg sacs were commonly found.

Differences in spider size and cannibalism

In the controlled laboratory experiment, in which hungry spiders were paired up to have size differences of 0mm-5mm, cannibalism occurred in 88% of the 40 total experimental pairs. Same sized spiders, spiders with a size difference of 0mm, composed 80% of the 12% of spider pairs that did not cannibalize. The likelihood of cannibalism occurrence decreased as with more size similarity among spiders. While spiders with a size difference of 1mm or greater had rates of cannibalism of 88-100%, only 50% of the same sized spiders cannibalized (Fig. 3).

In the pairs of cannibalistic spiders, an exponential fit curve model explains 28% of the data ($R^2= 0.288$, $RMSE=33.80$, Fit Curve Model, Fig. 4). There was a significant negative relationship between the time for cannibalism to occur and the size differences among pairs ($p= 0.0013^*$, $R^2= 0.272$, $RMSE= 0.665$, Linear Regression). The time for cannibalism to occur was dependent on the size difference between hungry pairs of

spiders. As the size differences among pairs of spiders increased, the for cannibalism decreased exponentially and leveled off among pairs with size differences ≥ 3 mm, in which the time for cannibalism was the same, less than 1 hour.

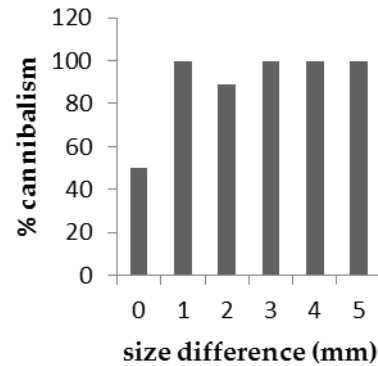


FIG. 3. Cannibalism among all pairs of spiders with size differences of 0mm- 5mm. This figure represents the 35 out of 40 total pairs that cannibalized. Percent cannibalism is based on the number of cannibalistic pairs within the total experimental pairs for each size difference, where n= number of experimental pairs.

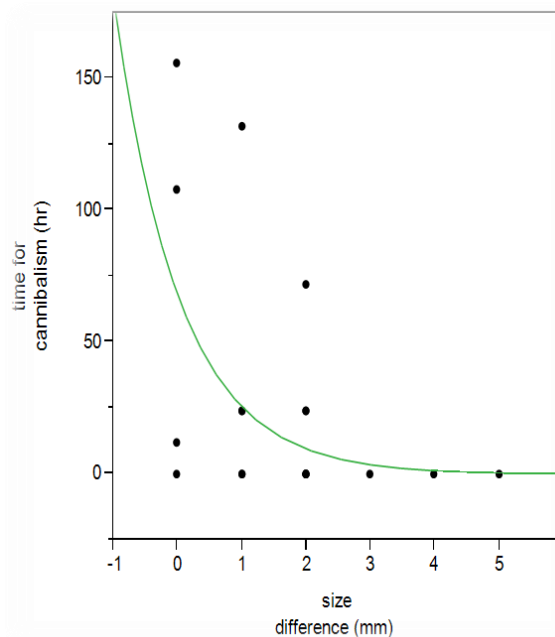


FIG. 4. Relationship between the time for cannibalism to occur and the size difference in pairs of spiders. Spider pairs that did not cannibalize (12.5%) are not shown in this figure. Each point represents a pair of spiders. Some points overlap.

Cannibalism and predation: prey size

When placed with a larger Surinam cockroach and a smaller spider, 63% of the medium sized spiders consumed the smaller spider first and the cockroach second. There was no preference for the smaller spider ($p=0.3173$, Pearson, $\chi^2= 1$, Fig. 5). In all 8 groups, both the smaller spider and the larger sized cockroaches were ultimately consumed by the medium sized spider.

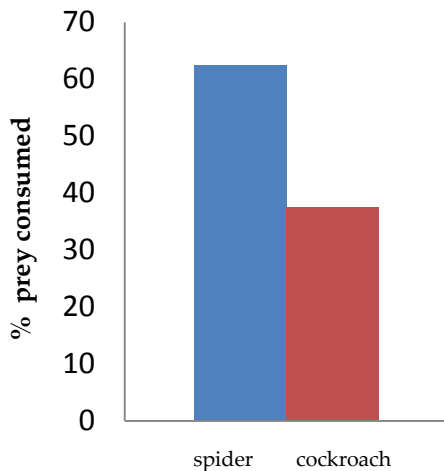


FIG. 5. Consumption of first prey by medium spider. Percent calculations were based on the total number of pairs (n=8).

DISCUSSION

This study reinforces the importance of size, as suggested by previous research, as a factor influencing cannibalistic and predatory behavior of wolf spiders. My findings contribute a more detailed aspect of size as such factor. Size differences between predator and prey were influential in the outcomes of

laboratory controlled cannibalism and predation experiments.

Differences in spider size and cannibalism

The results of this study disagree with my hypothesis, in which I predicted that cannibalism would occur in all spider pairs. A majority of the pairs with different sized spiders cannibalized, while only 50 % of the same sized spiders cannibalized (Fig. 3). In another study 64% of newly hatched pairs of wolf spiders (*Pardosa amentata*) that were the same size did not cannibalize and died of starvation (Hvam 2005). In my study I suspect that the spiders that died and did not cannibalize also died of starvation. In a different study on the species *Pardosa agrestis*, there was a significant positive correlation between the weight ratio of pairs, for pairs that differed in weight, and the occurrence of cannibalism (Samu 1999). In all of these studies cannibalism did not occur at a 100% rate, and cannibalism occurred at a higher rate in pairs of spiders that differed in body size or weight.

In this study, the significant negative relationship ($p=.0013^*$) between the time for cannibalism to occur and the size difference between pairs of spiders supported my hypothesis which stated that spiders that were more similar in size would take longer to cannibalize (Fig. 4). A threshold can be seen in the spiders that are more similar in size. The time for cannibalism to occur was also studied in *Pardosa pratigava* where the time for cannibalism to occur was shorter in hungry spiders as opposed to spiders that were not.

Overall, this study shares common trends with previous studies: there were lower rates of cannibalism and more time for cannibalism to occur in pairs of wolf spiders that were closer in size. Due to such similarities, I propose two explanations: 1) both size and hunger are important influences on cannibalism, and more so when combined as they were in this study, where cannibalism in different sized hungry spiders was studied

2) fear of retaliation, or the fear of failing when attempting to predate on same sized or larger prey, explains the longer time for cannibalism to occur in same sized spiders (Hvam 2005, Samu 1999).

Larger spiders are capable of surviving without eating for longer periods of time due to more nutrient and energy reserves. In this study, since pairs of same sized spiders ranged in sizes (i.e two 0.7cm sized spiders, two 0.9mm spiders, ect.) this reasoning for explaining why same sized spiders took longer to cannibalize does not apply. Again, fear of retaliation is a better explanation.

Cannibalism and predation: prey size

Although there was no significant predation preference ($p=0.32$) for the smaller prey by the medium wolf spiders, the observed trend, in which more than half of the medium spiders consumed the smaller spiders first and the larger cockroaches second, matched my expectation (Fig. 5). My prediction was derived from the fact that a rate of 100% cannibalism and a faster time for cannibalism to occur was observed in spiders with a size difference of 5mm which was the same size difference between the spiders used in this experiment. A similar study, in which two species of wolf spiders, *Hogna helluo* (Walckenaer 1837) and *Pardosa milvina* (Hentz 1844) were paired up with a spider and a cricket, results differed from those observed in this study (Rypstra 2005). In Rypstra and Samu's study both *H. helluo* and *P. milvina* were more successful in eating the alternative prey (crickets), which were larger than the wolf spiders. I offer a couple of potential explanations for why more medium spiders consumed the smaller spiders : 1) The medium spiders saw the smaller spiders first and therefore attacked and consumed the spiders over the cockroaches; 2) The medium spiders, which had already been previously deprived of food, predated on the smaller spiders first to ensure a successful meal.

Predating on the cockroaches first required more energy and would be more challenging to kill as a result of their larger size.

Conclusion and Future Directions

The abundance of spiders, their function as biological control agents for pests, and their role in imposing selective pressures, make these generalist predators important models for studying behavioral ecology (Uetz 1992). Wolf spiders in particular, are unique in their active foraging strategies and their cannibalistic tendencies. This study emphasizes the importance predator-prey size asymmetry as a factor that influences cannibalism and predation in wolf spiders under controlled laboratory conditions. This highlights the importance of hunting strategies used by these spiders to successfully predate on prey of all sizes in the wild, as was observed in the field.

In the future, improvements and follow up studies could enhance our understanding of the behavioral ecology of wolf spiders. Increasing the sample size of this study would be the first improvement. In addition, a study on the time for predation to occur across a range of other prey types and prey sizes could provide a comparative study to further understand the importance of predator-prey size differences. Other studies could focus on determining the preys that wolf spider consume in Mo'orea as well as the occurrence of cannibalism in the field. Lastly, investigating the cues that wolf spiders use to identify the size of their prey could enhance our knowledge about predator-prey interactions as well as cannibalistic behavior.

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