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ONE JUMP AHEAD: INTERSPECIES INTERACTIONS AND DISTRIBUTION OF JUMPING SPIDERS ON MO'OREA

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Abstract. Jumping spiders (of the family Salticidae) are found around the globe including on the island of Mo'orea, French Polynesia. Unlike continents, an island system such as Mo'orea often magnifies the effects of an invasive species due to their increased frequency of unfilled ecological niches. In my distributional study most species I encountered were non-native, and in my behavioral study I investigated the potential for correlation between a species' dominance in elevation-divided habitats and observed aggressive interspecies interactions. A total of 206 Salticidae were collected, 86 of which were utilized in my behavioral study. Of the eight jumping spider species encountered (six known, two unknown) I found there was no strong correlation between a species' behavior towards other spiders and its distribution. Future studies could be directed concerning how spider behaviors besides interspecies aggression influence the dominance of that species in a given habitat.

Key words: arthropods; Araneae: Salticidae; Moorea, French Polynesia; non-native; invasive; animal aggression; interspecific competition and communication

INTRODUCTION

In ecological systems worldwide, the biotic composition of any given habitat is influenced by many fundamental factors including energy availability, nutrient content, and climatic conditions. Besides these abiotic factors, traits of organisms inhabiting these environments can have great effect on population density and distribution of a habitat's flora and fauna. In island systems, these relationships can be particularly magnified given the increased availability of open ecological niches that may be utilized by a species whose native distributions might have been limited in their homelands by greater competition for resources.

Mo'orea (17°32'S 149°49'W) is the second tallest (1200m) of the Society Island chain of French Polynesia. Located 25km northwest of Tahiti, this island contains a vast variety of habitats with high degrees of species richness allowed by its dramatic climatic and altitudinal gradients. Though a number of plant and animal species were purposefully introduced by Polynesians with their arrival 3,000 years ago, the populations and influence of non-native organisms on native species did not reach detrimental levels until the arrival of Europeans in the 1700s (Meyer & Florence 1996).

Spiders of the Salticidae family are found the world over; inhabiting every continent

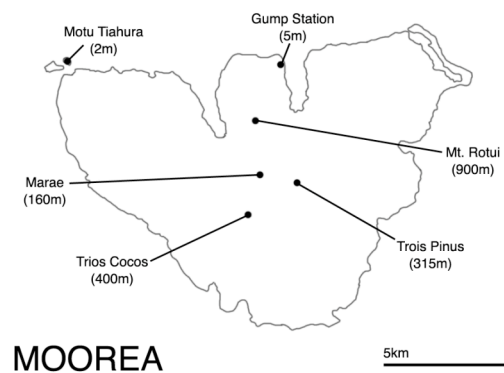


FIG. 1. Study sites of salticid distribution.

except Antarctica and every imaginable habitat at elevations as low as Californian salt marshes to as high as Mt. Everest (Witt & Rovner 1982). Salticid diversity is relatively high for an isolated Pacific island such as Mo'orea, however, the majority of these species are considered non-endemic as they occur on neighboring islands (Nishida 2008).

Colloquially known as "jumping," "hunting" or "wandering" spiders, members of the salticid family actively seek their prey, stalking them as felines do, instead of passively capturing them in a spun web. These congenial creatures are highly visual: observing any movement and approaching

any close object in a curious manner (Foelix 1996). Jumping spiders' dependency on sight for their lively hood explains their disposition as diurnal wanderers – though artificial lighting does allow individuals to remain active after sunset (Wolff 1980).

Interaction and communication in the spider world are decidedly linked to the morphology and physiology of any given species (Witt & Rovner 1982). Web-spinning spiders primarily rely on chemical and vibratory signals transmitted by the silken threads excreted by other spiders where hunting spiders, with their acute vision, communicate with one another primarily via displays of gesture and posture as well as exterior pattern and coloration. (D'Andrea 1987). Despite being visually oriented, creation and interpretation of substrate vibrations (instead of web vibrations) still play a crucial role in the mating behaviors and signals of many salticid genera (Elias 2005). Conspecific (with species) gestures that can be interpreted within a salticid's 25cm radius of vision as well as interpreted across salticid species are crucial in allowing jumping spiders to distinguish between fellow spiders and potential prey (D'Andrea 1987). Competitive and aggressive behaviors traditionally take place within a species when issues of access to mates, territory and rank within social hierarchy arise (Leimar 1988). Outside of mating pairs, cohabitation among salticids is uncommon with the exception of juvenile spiders occasionally found living together in large silk nests. Cohabitation can be prolonged between subadults until predatory behaviors develop or sexual maturity is reached (Witt & Rovner 1982, D'Andrea 1987).

Contests concerning territory often extend out of merely intraspecies and into interspecies interactions, as competition for resources such as ideal food and shelter is universal. As April Yang examined in 2008, consideration of overall spider diversity on Mo'orea demonstrates the near complete dominance of non-native spiders at low and mid-elevation habitats – the final refuge of native spiders being at less accessible high elevations. As increasing numbers of non-native jumping spiders occupy Mo'orea, I seek to investigate whether the most frequently found non-native species dominate habitats due to pronounced aggressive propensity.

METHODS

Distribution of Salticidae

A total of six sites categorized by relative elevation (low, mid, high) were chosen to survey salticid diversity on Mo'orea. Low elevation sites featured Motu Tiahura (2m) and Gump Station (5m). Mid-elevation sites featured the Marae trails (160m) and Trois Pinus "Three Pines" Lookout (315m) of the Opunohu valley. High elevation sites featured Trois Cocos "Three Coconuts" Pass (400m) and Mt. Rotui (900m). (Figure 1)

Collection techniques

Spider surveys were performed during daylight hours September through November, 2009. Two hours were spent at each site utilizing absolute and relative population sampling techniques – five minute insect net sweeps as well as thirty minute visual and manual searches of surroundings (vegetation, rock and boulder surfaces, and buildings when present) – respectively. All salticid spiders were identified to species (when possible); novel spider species were brought to Gump Station for further identification. Spiders 0.5cm and greater (to assure each spider's status as either adult or at least subadult) were collected in small plastic vials and brought to Gump Station for behavioral study.

Identification

Prószyński's diagnostic drawings library to Salticidae (2003) as well as Nishida's French Polynesia spider checklist (2008) were used in identification of spiders down to species. Unidentified spiders used in the behavioral study were given an alphabetical identifier. Detailed drawings, paintings, and macro photographs of all species included in the behavioral study were compiled into Appendix A. Voucher specimens preserved in 96% ethanol were deposited in the Essig Museum of Entomology at the University of California, Berkeley. [Note: voucher specimen labeled "Telamonia sp." is now considered unknown species A. Voucher specimen labeled "Euryattus sp." is now considered unknown species B.]

Interspecies interactions

Captured individuals were assigned an identification number and kept in their respective plastic vials. Each spider was fed

Drosophila (fruit flies) twice weekly to prevent the influence of hunger on the trials. Each spider was kept visually separated from the others with strips of copier paper to prevent premature visual communication between species. The length of each spider's cephalothorax and abdomen was recorded. Spiders were allowed at least three days to acclimate to the lab environment.

Trials were conducted in a discrete arena (Figure 2) that was small in size to eliminate potential territoriality and to ensure the mutual recognition of each spider as another spider and not potential prey. This consisted of a clear, undecorated, cylindrical glass cup with an internal height and width of 7cm x 7cm. The cup, along with a clear plastic lid, allowed for minimal visual distortion of the arena – useful for comprehensive observation and capture of quality video of each trial. A Canon Powershot G10 on a small tripod was used for recording video (high resolution, macro) of each pairing for further analysis.

For trials the arena was divided in half and given a level substrate, each made from custom fitted pieces of plain white copy paper. Each spider was introduced into either side of the arena for an acclimation period of two minutes. The divider was removed and the trials run for five minutes, after which the divider was replaced and the spiders returned to their respective vials. A spider killing the other spider in a time shorter than five minutes ceased the trial.

Each spider was paired with randomly selected representatives of at least two (but no more than five) different species. Shorthand notes during each trial recorded the frequencies of observed behaviors, defined in Table 1. Further analysis of video data was used to confirm and revise shorthand data.

FIGURE 2. Photograph of trial arena.



TABLE 1. Characterization of jumping spider interactions for the purpose of this study.

Behavior	Definition
Approach	walking or creeping of one spider towards the other
Retreat	fleeing of one spider away from the other
Attack	rapid leap of one spider on top of the other; contact without grasp
Deflection	defensive motion of the forelegs that blocks oncoming attack
Kill	an attack with a successful grasp and subsequent feeding

Note: Video examples of trials with annotated exhibited behaviors can be seen here: <http://www.youtube.com/watch?v=YaYv7XEI5ks> and here: <http://www.youtube.com/watch?v=gFpr9HUCvYk>

The arena and lid were washed with lab detergent and the paper dividers replaced after each trial to eradicate the presence of any chemical cues and web remnants.

Data analysis

Distributional and behavioral data was compiled in Excel 2003 and evaluated in JMP 2008. A Pearson's chi-squared test was performed to compare whether species abundance differed across elevation. A One-way Analysis of Variance (ANOVA) followed by a Tukey-Kramer HSD tested for any significant differences between mean approaches, retreats, attacks, deflections and kills across species.

RESULTS

Distribution of Salticidae

A total of 206 salticid spiders were encountered, 86 of those were included in my behavioral study. Six species were identified: *Thorelliola ensifera* (Thorell, 1877); *Plexippus paykulli* (Audouin, 1827); *Bavia aericaps* (Simon, 1877); *Menemerus bivittatus* (Dufour 1831); *Athamas whitmeei* (Pickard-Cambridge, 1877); and *Hasarius adansoni* (Audouin, 1827). (Population data can be found in Appendix B) All spiders identified to species in my study can be considered non-native and in many

cases are cosmopolitan, as is the case with *Plexippus paykulli* which is widespread in tropical climates (Nyffeler et al. 1980). These six species along with two unidentified species (A and B) were utilized in my behavioral study.

TABLE 2. Species with significant population distribution based on elevation.

Species	Pearson's chi-squared	DF	Prob>ChiSq
<i>Athamas whitmeei</i>	13.2308	2	0.0013*
<i>Menemerus bivittatus</i>	40.0000	2	<.0001*

Pearson chi-squared analysis of species populations (whose expected count was greater than five per elevation) yielded mostly insignificant differences; those with significance are detailed in Table 2. *Athamas whitmeei* are very likely to be found in mid and high elevation habitats as opposed to low elevation ones. In this study *Menemerus bivittatus* was exclusively found in low elevation habitats.

Interspecies interactions

A one-way ANOVA of found that neither average attacks nor average kills across species were significantly different (attacks $F=1.8266$, $P=0.0938$) (kills $F=1.9334$, $P=0.0753$). However, average approaches, retreats, and deflections did yield significant data (approaches $F=4.0536$, $P=0.0008^*$) (retreats $F=2.6005$, $P=0.0182^*$) (deflections $F=15.767$, $P<0.0001^*$).

Tukey-Kramer HSD testing for difference between particular species resulted in some significant data for approaches, retreats, attacks, kills and a greater quantity of significant data for deflections. *Plexippus paykulli* and species B had significantly more average approaches than *Thorelliola ensifera*. *Menemerus bivittatus* had significantly more average retreats than *Thorelliola ensifera*. On average, *Plexippus paykulli* was more likely to attack as well as more likely to kill than *Thorelliola ensifera*. The breakdown of difference between average deflections proved the most compound; *Athamas whitmeei*, *Bavia aericeps*, species A and species B all showed significantly greater propensity to deflect

attack than *Menemerus bivittatus*, *Plexippus paykulli*, and *Thorelliola ensifera*.

TABLE 3. Rank of longest to shortest average cephalothorax plus abdomen length

Species	Average length(mm)
<i>Plexippus paykulli</i>	11.1
species B	10.4
<i>Bavia aericeps</i>	8.7
<i>Menemerus bivittatus</i>	7.9
<i>Hasarius adansoni</i>	7.2
species A	6.5
<i>Thorelliola ensifera</i>	6.3
<i>Athamas whitmeei</i>	5.8

DISCUSSION

Distribution of Salticidae

Due to their already widespread distribution across the globe, it is often difficult to ascertain which species of jumping spiders are native to any particular locale. While it is safe to assume the non-native status of the six species I encountered (given their known distributions in other areas of the world, namely the Pacific islands west of Mo'orea as well as Asian continent) the two other species I encountered (species A at low elevation, species B at high elevation) I was not able to identify down to genus, even morphologically referring to genera already found within the Pacific islands (Nishida 2008, Prószyński 2003). This demonstrates the possibility that salticid diversity throughout these islands is still not fully understood, and further surveys of spider populations would be prudent. There is also the possibility that the unknown species I encountered were result of adaptive radiation of a known genus, which could be confirmed by molecular analysis of their genetic makeup. Where the distribution of *Menemerus bivittatus* coheres to the trend of non-native species to overtake low elevation coastal habitats (Yang 2008), the significant population data of *Athamas whitmeei* is curious as it is found primarily at mid to high elevations. Considering the genus *Athamas's* global distribution is focused within the Pacific islands, this unusual non-native distribution could be attributed to habitat preferences of this genus; perhaps it prefers densely forested inclines.

Interspecies interactions

Though significant trends exist in comparing qualitatively aggressive behavior among non-native species, they do not equate to dominance within a given habitat. As seen with *Plexippus paykulli* and *Thorelliola ensifera*, *P. paykulli* averaged more attacks and kills than *T. ensifera*. However, *T. ensifera* had the highest encountered population out of any species with 78 total individuals and was the dominant species in 5 out of 6 sites (Appendix B), indicating factors other than domineering behavior are at work. The increased likelihood of *Menemerus bivittatus* to retreat from another spider could perhaps be linked to its limited, low-elevation distribution.

Reflecting on the overall significant data concerning approaches, retreats and deflections, further investigation into methods of arachnid communication brings to light some important considerations. Jumping spiders, who do not create silk-transmitted signals (vibratory or chemical) lack the web-spinner specific messages that allow for remote communication of identity and therefore non-contact driven tolerance of other spiders (D'Andrea 1987). They rely primarily on visual cues, and if aggressive behaviors such as attacking and killing conspecifics were the norm at any point in evolutionary time, natural selection would eventually eliminate spiders with these greater belligerent inclinations (as fighting to such a degree causes loss of life or reproductive fitness) (Witt & Rovner 1982). Consequently, non-violent behaviors that indicate affinity for visual investigation before action (approaching) and generally discouraging contact (retreating) would be selected for and hence more prevalent among jumping spiders. Non-reproductive behaviors such as universal threat postures among salticid genera are well documented in reducing cannibalism as they increase the ability of another spider to recognize its kin. This however should not imply that competition is irrelevant to jumping spiders – in fact regular spacing and density of spiders within any given habitat depends greatly on these non-violent displays and contests (Witt & Rovner 1982). Casual observations of my trials also attest to these notions, as often trials yielded little or no interaction whatsoever with the spiders either completely ignoring or avoiding one another. Trials producing the largest quantity of described interactions were between spiders

of comparable size, and this lends well to the purposes of my study as this data would be more interspecies-based rather than size-dependent. Size dependency most likely did have some effect on my study, as some species were on average larger than others, allowing them to antagonize species of smaller average size (for example *Plexippus paykulli*, who performed most aggressively during my trials, also had the greatest average body length (Table 3).

Though my study indicates aggressive propensity does not significantly contribute to salticid distribution on Mo'orea there is great potential for study of the potential presence of particular characteristics that would allow for species to become dominant in a variety of habitats across the Society Islands as well as the globe.

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APPENDIX A

Illustrations & Photographs of encountered Salticidae by Danielle Peña
 (one grid square in photographs = 2mm²)
 Additional photographs, full color versions available at:
<http://www.flickr.com/photos/artmouse/sets/72157622890455823/>

Thorelliola ensifera



Predominantly brown (female) or black (male) with dense golden-colored, iridescent hairs. Carapace "horn" consists of two long, spine-like fused setae. There are three small, circular, white tufts of hair along the rear edge of the abdomen.

Plexippus paykulli



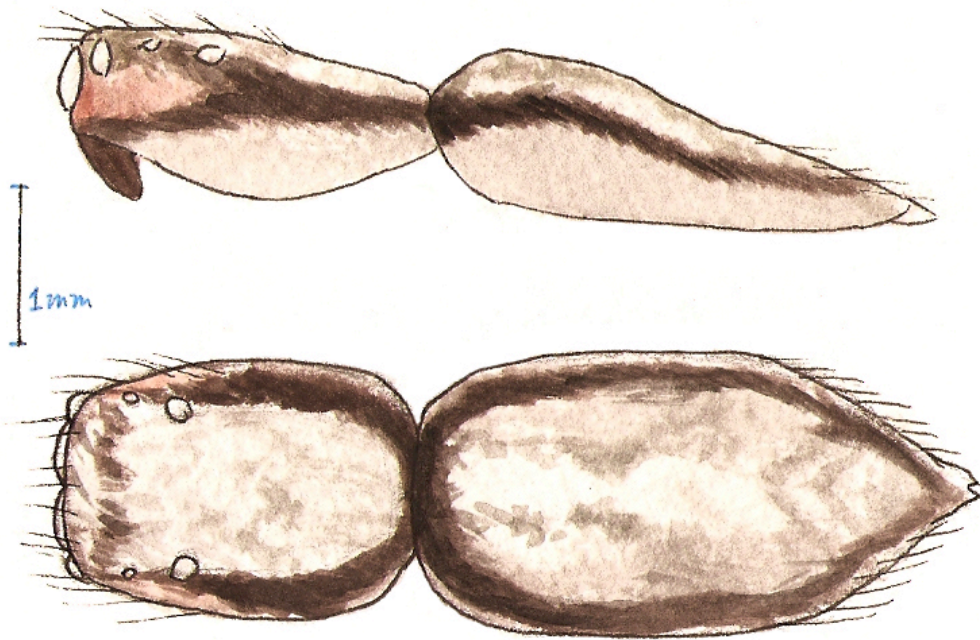
Medium brown with a broad white median band, continuing the one on the carapace and almost reaching the spinnerets. The sides of the abdomen are white. At about a third of the way from the spinnerets there are two characteristic circular white spots.

Bavia aericeps



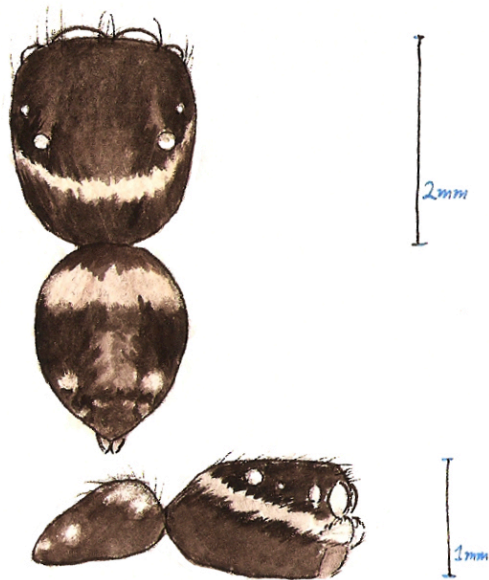
For the male of the common *B. aericeps*, the cephalothorax is broad and flattish, and in plan is slightly longer than wide. The abdomen is long and tubular, rounded at the anterior end and tapering to the spinnerets. The female has a brown abdomen with a broad, median, yellow stripe.

Menemerus bivittatus



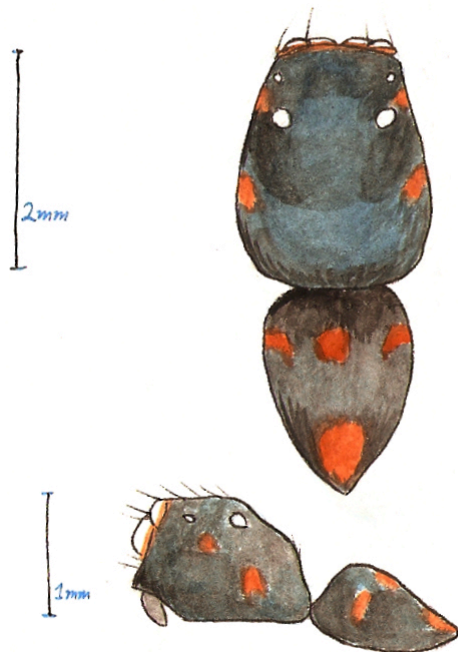
Overall the abdomen is whitish-brown with a broad, dark brown, median band running the length of the abdomen. The female is overall brown with a very broad whitish-brown band that runs from the front eyes to the spinnerets.

Hasarius adansonii



The dark brown eye area and carapace of the male *H. adansonii* is bordered by a light, crescent-shaped area carrying white hairs. Around the cephalothorax there is a white crescent-shaped collar. Towards the rear there is a vague, broad lightish area in the middle and several white spots, two of which are prominent. The female is a lighter edition of the male and the white spots on the abdomen are not evident.

Athamas whitmeei



Species A: (*juvenile, adult, adult, adult*)



Species B:



APPENDIX B

Raw population data of identified species by site and elevation

Site	Elevation	<i>Thorelliola ensifera</i>	<i>Bavia aericeps</i>	<i>Athamas whitmeei</i>	<i>Plexippus paykulli</i>	<i>Hasarius adanoni</i>	<i>Menemerus bivittatus</i>
Gump Station	5m	23	4	0	6	3	5
Motu							
Tiahura	2m	10	2	0	3	0	15
Marae	160m	19	0	12	5	0	0
Trois Pinus	300m	6	0	2	4	0	0
Trois Cocos	400m	13	0	12	4	2	0
Mt. Rotui	900m	7	0	0	2	0	0