Free Water Fuels Intraguild Predation in a Riparian Food Web

by

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A Thesis Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

Approved November 2015 by the
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ARIZONA STATE UNIVERSITY

December 2015

ABSTRACT

In desert riparian ecosystems, rivers provide free water but access to that water diminishes with distance producing a steep gradient in the relative importance of water for growth and reproduction of riparian animals and hence, their biodiversity. Previous work suggests that water limited riparian predators eat more prey to meet their water demand where free water is not available. Here I explore the effect of water limitation on prey selection and per capita interaction strengths between a predatory spider (*Hogna antelucana*) and two prey species occupying different trophic levels using a controlled field experiment conducted in the riparian forest of the San Pedro River, Cochise County, AZ. Lab measurements of water and energy content revealed that intermediate predators (smaller spiders in the genus *Pardosa*) had 100-fold higher energy: water ratios than an alternate prey species more basal in the food web (crickets in the genus *Gryllus*). Given this observation, I hypothesized that water-stressed predatory wolf spiders would select more water-laden crickets but switch to more energy rich *Pardosa* when water stress was experimentally eliminated. Additionally, I hypothesized that switching by quenched *Hogna* to *Pardosa* would reduce predation by *Pardosa* on *Gryllus* leading to increased abundance of the basal resource. Finally, I hypothesized that water mediated switching and release of basal prey would be stronger when male *Hogna* was the apex predator, because female *Hogna* have higher energetic costs of reproduction and hence, stronger energy limitation. Experimental water additions caused both sexes of *Hogna* to consume significantly higher numbers of *Pardosa* but this difference (between water and no-water treatments) did not vary significantly between male and female *Hogna* treatments. Similarly, strong negative interaction strengths between *Hogna* and *Pardosa* led to

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release of the basal prey species and positive interaction strengths of *Hogna* on *Gryllus*. Again strong positive, indirect effects of *Hogna* on *Gryllus* did not depend on the sex of the *Hogna* predator. However, water mediated indirect effects of *Hogna* (either sex) on *Gryllus* were the strongest for male *Gryllus*. These results suggest that water and energy co-dominate foraging decisions by predators and that in managing water-energy balance; predators can modify interaction pathways, sex-ratios of prey populations and trophic dynamics.

DEDICATION

John Sabo our fearless leader

Karl Wyant for keeping it real

Kim Michel for support

Michael Quinland for late night cage surveys,

Dustin Lisiewski for field work and location expertise

Robin Greene for excellent field assistance and laughs.

Daniel Allen special thanks for cages and materials

Martin Vega was the backbone of my infrastructure

Sandy Anderson and the Grayhawk Nature Center

Eric Moody, Kevin McCluney for ideas

Cornelius Klok a fellow naturalist

Jenny Nellsch keeping us stocked

Renelle for believing in me

Karla Moeller for methods

Jon Harrison for his lab

Chadwick Johnson

Denise Johnson

Scott Bessler

Albert Ruhi

N.S.F.

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Introduction

Water can alter community structure and trophic dynamics both indirectly via

stimulation or limitation of primary production (Huxman et al. 2004), and directly via the

influence of free water availability on foraging behavior (Noy-Meir 1973, Golightly and

Ohmart 1984). In semi-arid terrestrial settings, recent work has shown that animals often

dramatically alter foraging behavior to balance water and energy intake (McCluney &

Sabo, 2009; Spiller & Schoener, 2008; Wolf & Martinez del Rio, 2003). In these studies,

consumers eat more prey to meet their water demand when free water is limiting thereby

balancing individual water budgets and enhancing per capita interaction strengths on

water-laden prey; however, little is known about the energetic implications of such water-

mediated foraging choices (Noy-Meir. 1973, 1974) suggesting that animal species in arid

lands are jointly limited by water and energy. Hence, predators should switch between

water- and energy-rich prey species depending on the relative strength of water and

energy limitation. In this thesis, I explore this question in the context of omnivory and

intraguild predation to understand how water limitation determines the trophic position of

preferred prey by top predators.

Intraguild predation (IGP) is defined as consumption between potential competitors

that share a basal resource (Polis; Polis and Strong 1989.). Intraguild predation is one of

several trophic interactions that create reticulate motifs lending enhanced stability to the

larger food web (Fagan; Bascompte et al.). In desert food webs reticulate motifs in

apparent competition, cannibalism and omnivory also include IGP (Polis 1991; 1994). In

a meta analysis of 599 studies of food webs, IGP was identified in 86.7% of them

underscoring the ubiquity of this trophic motif (Arim & Marquet 2004). Intraguild predation affects community structure directly with either symmetrical (i.e., -/-) or asymmetrical (i.e., -/0 or -/+) outcomes. The effects of IGP differ from apparent competition because of direct predation between predators (Polis et al.1989). Predation of intermediate predators can also lead to behavioral changes of the respective intermediate predator that can influence attack rates on shared prey and hence, community structure more than direct mortality caused by the top predators (Polis.1994). Though the effects of IGP on predator and shared prey species abundance have been well explored in both theoretical and field settings, less is known about the physiological drivers of predator foraging decisions, and hence the propensity and context dependency of IGP in a community.

One promising framework for predicting IGP is stoichiometry. Nitrogen limitation by predators may drive them to eat higher on the food chain (engage in IGP) and/or cannibalism because predators tend to have lower C:N than prey in the same ecosystems (Fagan et al. 2002; Denno and Fagan 2003; Fagan and Denno 2004; Matsumura et al. 2004). Though, this work has met some substantial criticism (Wlider and Eubanks 2010 and references therin), the framework is potentially powerful and transferable to other sets of resource limitation. Here I explore a similar idea but in the context of co-limitation of predators by water and energy. Specifically, I ask how the availability of free water influences the propensity of top predators to eat energy-rich intermediate predators vs. more water-rich basal prey. I hypothesize that predatory wolf spiders select water-rich prey species lower on the food chain when they are water stressed because these resource species have higher water to energy ratios than intraguild predators. I

similarly hypothesize that these same predatory spiders will switch to intraguild predators (a different spider species) when water stress is experimentally reduced because intraguild spiders have a higher relative energy content (lower water to energy ratios). Finally, I hypothesize that experimental reduction of water stress will benefit prey species because intraguild predation (spiders eating spiders) reduces total predation pressure by spiders on basal prey as a result of switching (by top predators) and increased mortality of intraguild predators.

Finally, female and male predators should be subject to different energetic constraints due to costs of reproduction—female egg production, and/or behavior, and higher levels of aggression for mate selection by males defending large territories. Pursuing this nuance, I ask whether there is sexual dimorphism in either IGP by the top predator and how intersexual variation in water/energy content of the basal prey influences this. I hypothesize that IGP by female predators will be more robust to variation in water stress because female spiders have higher energetic costs associated with gamete production and provisioning of offspring. Moreover, I hypothesize that water-stress will drive top predators to eat more male prey because males have higher relative water content than females of the same species.

Methods

The San Pedro River is an undammed free flowing river from Mexico in Southeast Arizona. The study area falls within this riparian cottonwood forest gallery. The river has a variable annual flow rate that changes the landscape annually during monsoon season

(late July to Sept.). Boasting over 250 migratory species and 80 species of mammals, it is among the most ecologically important rivers in the United Sates. This study was located in a variable cottonwood forest gallery between Charleston bridge and the Gray Hawk Nature Center adjacent to the SPR. The cages were placed in typical conditions of this area, composed of cottonwood trees, approx. 30% small to medium dry grasses and a sandy loam matrix The field study occured in the summer from May 2 e July 6, 2012. Day temperatures ranged from 27-37°C with the mean peak temperature at 35°C. Night temperatures ranged from 15-21°C with the mean low a 11.6^{O}C. Soil moisture ranged from 3%-12% and there were no insidence of rainfall during the three trials. Temperature measured and averaged between six HOBO© Micro Stations with radiation shields. Respective species used for study included readily abundant species used in previous studies (McCluney. 2009), namely *Hogna antelucana* distinguished by sex and sampled in equal ratios, *Pardosa* sp., and Gyllus, distinguished by sex and sampled in equal ratios.

Laboratory Measurement of Prey Water and Energy Content

Gravimetric Water Content—Gravimetric methods were used to quantify water content (mg/mg) of arthropod prey and predators. Arthropods were collected in the evening and frozen in pre-weighed glass poly-seal vials with lids within one hour of capture. Six (6) samples (free of defect, lost limbs) of each species were processed. Species where *Hogna antelucana* (male and female) *Gryllus alogus* (male and female) and *Pardosa* sp. All animals frozen for gravimetric measure were dried to a constant mass at 65°C for a

minimum of 12 hours. Dry masses were re-weighed for calculations and re-dried in preparation for bomb calorimeter protocols.

Calorimetry—Bomb calorimetry was used to determine energy content (kJ/mg) of arthropod predators and prey. Dry masses of field spiders previously evaluated for TWL by gravimetric procedures were prepared individually into pellets of approximately .05g at time of calorimeter samplin*G*. Sample in cue placed within a large desiccator to prevent ambient rehydration. Calorimetry was achieved using a Parr model 1425 Semimicro Calorimeter standardized using benzoic acid pellets per sample. All samples and standards were run in double and averaged to prevent machine bias/error. Unexpired Fuse from samples was weighed and samples corrected as per protocol. Oxygen used to fire the fuse was 100% Oxygen and the distilled water to encase the bomb was at room temperature. The electrodes that sparked the fuse were brushed clean prior to each sample run. Fuse wire was No.45C10 at 2.3 cal./cm.

Field Experiment to Compare Interaction Strength of Intraguild Predators

To quantify the effects of free water availability on IGP in this arthropod community, I designed and executed a field experiment of 24 cages of five treatments and two levels (Table 1). This study isolated large predatory spiders (*Hogna antelucana* by sex into cages (in unity) of 2mx2mX2m (Fi*G*. 1) with a suite of prey treatments.

Table 1. Experimental Design - Treatments / Levels

Field Study	Legend:					
	Primary predator		Basal Prey		Intermediate Predator	
	Hf: H. antelucana female		Gf: G. alogus female		P: Pardosa sp.	
	Hm: H.antelucana male		Gm: G. alogus male			
Levels	Treatment 1	Treatment 2	Treatment 3	Treatment 4	Treatment 5	
	Hf/Gf/P	**Hf/Gm/P**	**Hm/Gf/P**	**Hm/Gm/P**	**Cm/Cf/P**	**Sum totals**
H20 cages	9	7	7	6	7	36
NO H20 cages	5	8	8	9	6	36
Total cages	14	15	15	15	13	72

To manipulate water availability, Zilla© water pillows that hold ~ 30 g of free water (described in Sabo et al. 2008; McCluney and Sabo 2009) were used. Treatments were applied to 2 m high enclosures (Figure 1) with a basal area of 4 m2 (2m x 2m footprint). Eight enclosures were constructed in each of three sites (not more than 10m apart) within 10m of the wetted channel of the river in a reach of the San Pedro where previous work on the same spiders has been done (Sabo et al 2008, McCluney and Sabo 2009). Enclosures were constructed of ½ inch PVC frames draped with sewn one-piece mesh covers and had a velcro sewn door on one elevation for re-entry and proper sealin*G*. The base of the PVC with the mesh attached (wrapped and zip tied) was buried in a perimeter no less than 25cm deep in surrounding soil. The the enclosures' floor was consistent across enclosures and with the adjacent riparian gallery habitat.
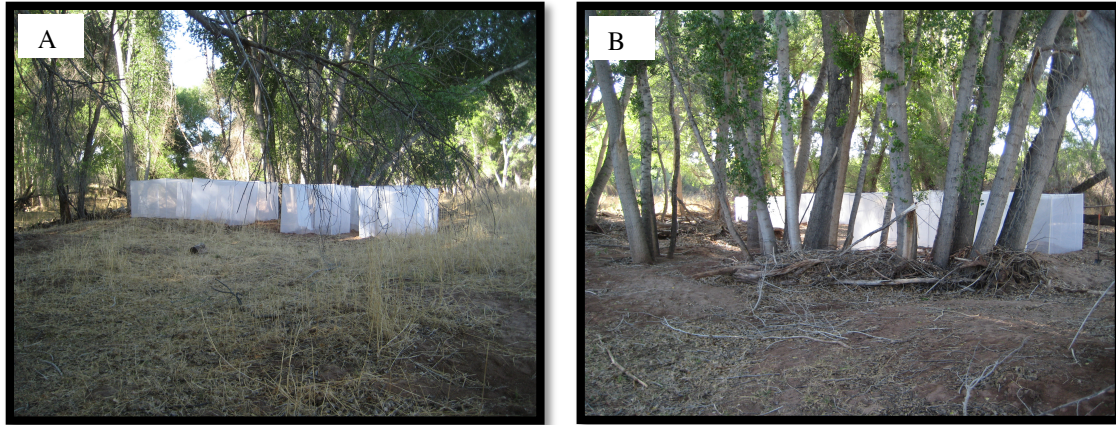
Figure 1. A Open grass habitat with cages organized by quads. Each at 2mx2mx2m. B. Under canopy cages organized by quads. Each at 2mx2mx2m

Cottonwood leaf litter was removed from all cages. Litter was restocked to a constant depth of 4-5 cm, after removing all arthropods by sun drying litter between two thermo-reflective silver tarps. Temperatures within the tarps measured at a minimum of 140^OF. Leaf litter hosts fled via escape pleats lower than the tarp. Close inspections revealed that all leaves were void of arthropods. In addition to rationed leaf litter, each cage received a 20cm x 30cm x 3.75cm flat, non painted lumber (fir) used as a proxy of large woody debris common in the understory and used frequently by arthropods as refuge from midday heat.

All cages were supplemented nightly with two fresh cottonwood leaves as a food source for *G. alogus*. Leaves were selected of similar size (+/-2cm) and chlorophyll quality estimated by coloration. Half of the enclosures were randomly designated for water supplemented trials and received a single 30g silica gel hydration Zilla© water pillow. Water pillows in water supplemented cages were removed and replaced fully hydrated every twenty-four hours. Water source was from the San Pedro River- collected fresh from clear water daily.

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The night prior to the experiment, all arthropod subjects were captured by hand. Collection quantities were thirty-six (36) *H. antelucana*, fifty-four (54) *Pardosa sp.* and sixty (60) *G. alogus* at sites along the river but not in direct proximity to the cages (min.100 meter distance). Spiders were kept isolated to prevent attack/ damage or unnecessary stress. Of this quantity, six (6) of each species were frozen and weighed in pre-weighed polyseal vials for future gravimetric studies. The remaining spiders and prey were marked with fluorescent acrylic paint markers and used in the trials. Color codes that corresponded to labeling sex and treatment designation identified the combination per cage.

Pre-trials of spider satiation were used to determine ambient prey density to avoid predator starvation or stress. We added a single *H. antelucana* (sex depending on treatment level) to all of the cages except those serving as controls (half of the cages received males and the other half females). Prey additions were two 1.5 cm diameter *Pardosa* sp. and two *G. alogus* (also separated by sex in equal ratios between trials). In this experiment, I relied on predator (*Hogna* a.) free controls to differentiate predation (*Hogna* induced mortality) from natural ("background") mortality. Control cages were free of *Hogna*, but had all possible prey including, two (2) *Pardosa*, and two (2) male and two (2) female *G. alogus* (four total). Trials were continued for 96 -100 hours at which time, we surveyed predator and prey abundances to estimate interaction strengths.

At the end of each trial, I identified and captured all living experimental subjects. Ultraviolet fluorescence by use of U.V. flashlights made host very easy to spot. The consistency of leaf litter, and proxy wood/log also made the timed searches very effective with a recapture rate in excess of 80%. Searches were timed at 15 mins per cage and a

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team of four took approx. 90 mins to complete each survey. Cages were also inspected by day for intruders and occasional diurnal arthropods were identified and removed. Invasion by non-target species was very low. I executed up to 9 replicates of each of 10 treatment combinations (N = 72) in sets of three experimental trials. In doing this, I attempted to balance the design by treatment and time, but was not always successful.

Estimation of Interaction Strength

Dynamic interaction strengths were estimated following Wootton 1997 and Berlow et al. 1999 :

$$\alpha = -\ln\left(R_0 \middle/ R_C \right) C$$

where alpha is per capita interaction strength, R_0 is resource abundance in the control enclosure, R_C is resource abundance in the experimental enclosure (with consumer, C), and C is consumer density in the enclosure (here always unity). Due to logistic constraints, control treatments (n = 13) were not paired with every experimental treatment replicates (n= 61) in space or time. Instead, mean control survival ($\overline{R}_C$ in water or no-water treatments) was used to correct predation estimates for natural mortality.

Results

Energy contents were highest for female *Gryllus*, regardless of sex. *Pardosa* had the lowest energy content of all resources, and was the only resource with lower per capita

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energy content than male *Hogna* (Figure 2).   Water contents followed a very similar pattern (but were extremely low for *Pardosa*). As a result, the energy to water ratio of *Pardosa sp.* is > 100-fold higher than *Gryllus* (either species; Fig 3.) and lowest (near unity) for male *Gryllus*.
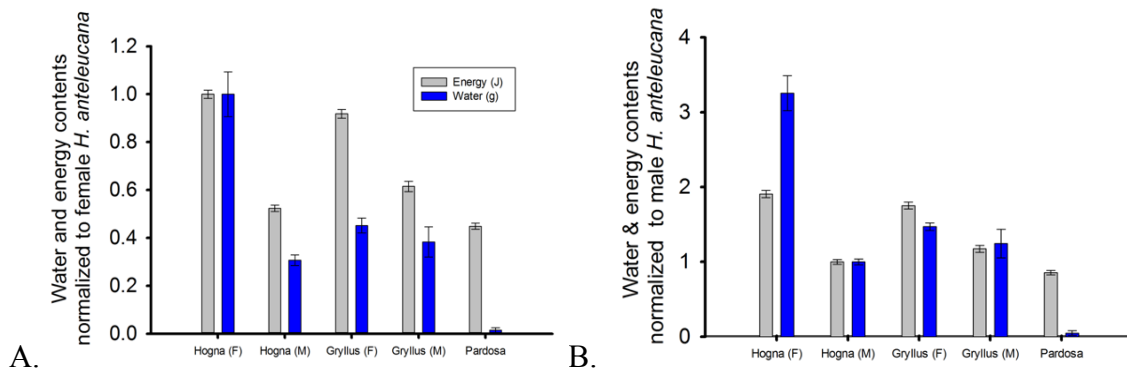
Water-Energy Content of Resources

Figure 2. Energy (kJ) and water (g) contents of prey species normalized to respective primary predators by sex: female (A.) and male (B.) (*H. antelucana*). Per capita energy to water ratios derived from gravimetric methods to determine total water content per gram and bomb calorimetry to derive caloric energy (kJ) content per gram. Note: Female spiders and crickets used in the study are sexually mature gravid specimens.
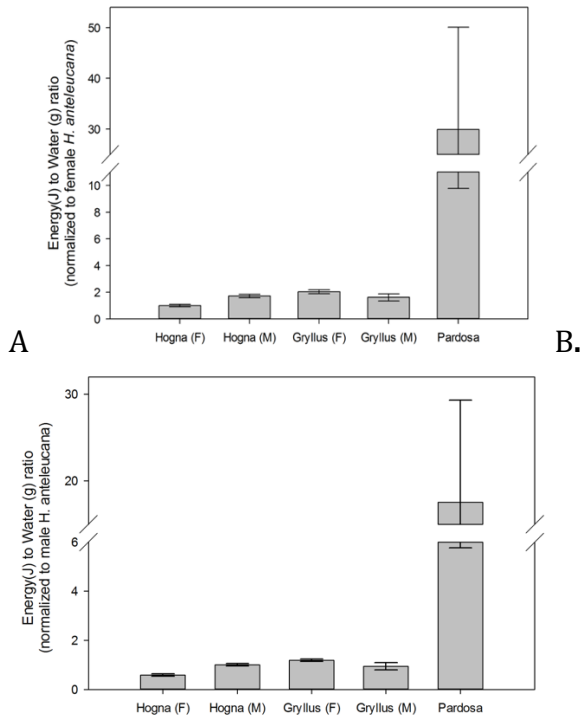
Figure 3. Comparative ratios of Energy (kJ) to water (g) normalized to normalized to respective primary predators by sex: female (A.) and male (B.) (*H. antelucana*). Note that intermediate predator per gram provides 100-fold the energy value of all other prey compared to very low water.

Intraguild Predation and Experimental Interaction Strength

Experimental additions of free water via water pillows significantly altered foraging decisions by *H. antelucana* leading to higher per capita predation of *Pardosa* (i.e., greater IGP; Figure 4a; Table 2). This result did not differ between male and female *Hogna* (Figure 4a; Table 2). Consumption of small spiders when water was added led to strong *positive* per capita effects of *Hogna* on *Gryllus* (Figure 4b; Table 3). This effect was stronger for male than female *Gryllus*. These results suggest that water and energy co-dominate foraging decisions by predators and that in managing water-energy balance, predators can modify interaction pathways.
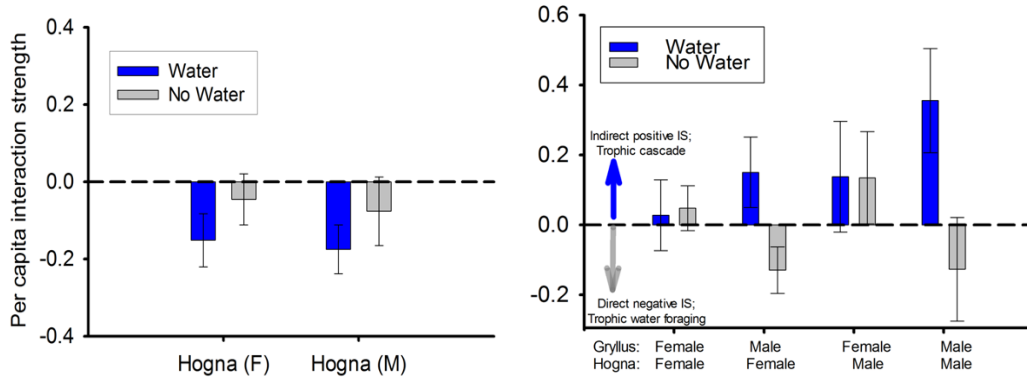
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Figure 4. Interactions effects (A) between the primary predator (*H. antelucana*) and the intermediate predator (*Pardosa* sp.). Negative effects increase with free available water regardless of respective sex. (B) Interactions between *H. antelucana*, and the basal resource. Positive effects imply relaxed predation and a trophic cascade.

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Analysis of Variance Table

Response: Effects on small spiders (Pardosa)
                        Df  Sum Sq   Mean Sq F value  Pr(>F)
H2O                      1 0.14546 0.145465  6.4427 0.01424 *
Hogna (+/-)              1 0.01077 0.010769  0.4770 0.49293
Prey (Cricket sex)       1 0.00391 0.003911  0.1732 0.67901
H2O:Hogna                1 0.00030 0.000303  0.0134 0.90826
H2O:Prey                 1 0.00056 0.000563  0.0249 0.87512
Hogna:Prey               1 0.00115 0.001153  0.0511 0.82210
H2O:Hogna:Prey           1 0.05407 0.054065  2.3946 0.12794
```

Table 2. Results from linear mixed effects analysis of water and predator (*H. antelucana*) effects on intraguild predators (*Pardosa sp.*).

Analysis of linear mixed effects on prey variables (*Pardosa* sp.) show significance (Table 2) of water limitation on interactions (predation) from Primary predators (*H. antelucana*). Basal prey effects most significant are Water and prey treatments corresponding to male basal prey (*G. alogus*).

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Analysis of Variance Table

Response: Effects on crickets (G. alogus)
                        Df  Sum Sq Mean Sq F value   Pr(>F)
H2O                      1 0.47991 0.47991  8.1797 0.006124 **
Hogna (+/-)              1 0.16531 0.16531  2.8175 0.099358 .
Prey (Cricket sex)       1 0.01248 0.01248  0.2128 0.646568
H2O:Hogna                1 0.03883 0.03883  0.6618 0.419717
H2O:Prey                 1 0.55503 0.55503  9.4601 0.003372 **
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Hogna:Prey                        1 0.00009 0.00009   0.0015 0.969342
H2O:Hogna:Prey                    1 0.02877 0.02877   0.4903 0.486971
Residuals                        51 2.99222 0.05867
```
Table 3. Results from linear mixed effects analysis of water and predator (*H. antelucana*) effects on basal prey (*G. alogus*).

Discussion

   Intraguild predation (IGP) has been shown in previous theoretical work to be an important motif in food webs that can determine stability ; however, little is known of the relative prevalence of intraguild predation in larger food-webs. Results from these experiments suggest that water is a potentially robust driver of IGP and that water mediated decisions (in terms of prey selection) can dramatically alter trophic dynamics. Specifically, primary predators eat higher on the food chain when water stress is experimentally relieved with free water, thus exerting stronger predation pressure on intermediate predators. This water mediated IGP in turn releases basal resources (crickets) from predation pressure from both top and intermediate predators leading to cascading effects (Figure 5). Observed, water mediated cascades were most pronounced for treatments in which the basal prey species was a male rather than a female cricket (Fi*G*.4). In summary, water consistently catalyzed an asymmetrical IGP interaction suggesting that this currency may drive the population effects of top predators (*Hogna*) on abundance of smaller spiders and sex ratios of basal prey species.
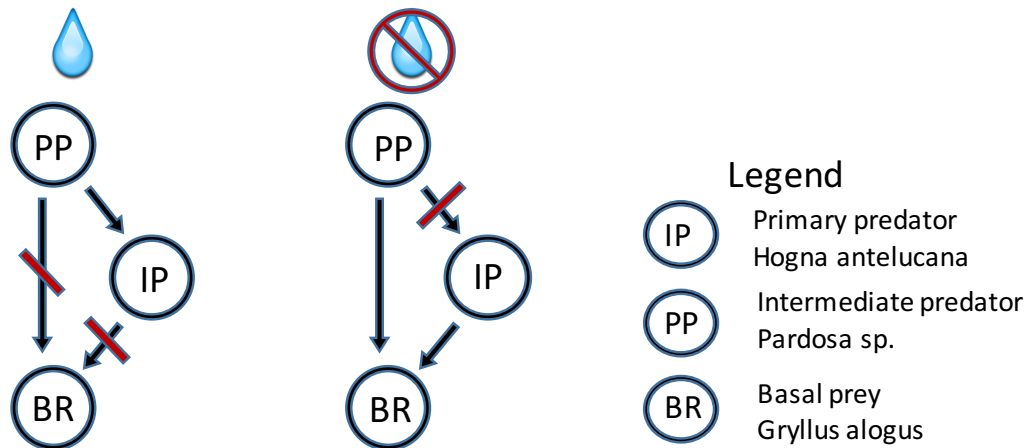
Figure 5. A) No water stress of the primary predator results in IGP and leads to cascading effects; particularly significant for basal prey (male crickets).
B) Water stress of the primary predator leads to exploitative competition (no IGP) in an asymmetrical interaction between basal resources (male crickets) and H. antelucana.

Male cricket mortality (predation) was highest (among all prey studied) in non-water supplemented treatments. This interaction is supported by the hypothesis that; big spiders select water-rich crickets lower on the food chain when they are water stressed because these resource species have higher water to energy ratios than small spiders. A possible explanation for *H. antelucana* preference of male crickets may be due to increased vibrations resulting from mating call stridulating *Gryllus*. Gryllidae stridulation has been noted to lead to increased predation on males (Robinson & Hall.2002). This may be one possible explanation for increased male basal predation selection by *H. antelucana*. Another possible explanation is the dietary pause commonly observed among arachnids post ingestion (Leinbach, *unpublished data*). During the reproductive season, female *Gryllus* are gravid. Female *Gryllus* was found to yield the highest energy to water ratio (almost matching that of predatory female *Hogna*). This increased energy ratio may account for the increased pause require to balance nutrient intake and body

pressurization. This explanation has implications for body mass ratios and optimal diet index in regards to foraging optimization. This shift in segment allocation, by *Hogna*, led to positive indirect effects or a trophic cascade. However, I only studied these effects within a single guild. Intraguild predation is observed between the primary predator (*Hogna antelucana*) and the intermediate predator (*Pardosa* sp.). Young *Hogna* are preyed on by *Pardosa*, and *Pardosa* preyed on by mature *Hogna*. They share the basal resource *Gryllus* and attack rates have been observed to correspond to body size (Barnes et al. 2010). This interaction may affect *Gryllus* abundance and behavior, however this was not tested in this study. I found that water availability mediated intraguild predation. When free experimental water was present, *Hogna*, regardless of sex, selected for the intermediate prey, thus relieving pressure on the male basal prey. This is interesting because distributions of prey shift with water availability. This patchiness may also affect male cricket stridulating and sexual behavior. Water and energy colimitation had a strong influence on IGP interactions within guilds leading to foraging decisions of IGP predators that altered trophic dynamics. IGP can lead to alternative stable states and other research has found IGP to have more impacts on population dynamics than predation or completion alone (Polis et al. 1989).

Estimating community structure through interaction strength, community ecologists have had a difficult time agreeing on measures that would most accurately describe consumer resource interactions. Field studies are typically limited in terms of food web chain lengths and naturally occurring trophic complexity (McCann.2000). Short term experiments are necessary to estimate community interactions and field experiments with including longer portions of the food web are the best way to understand the complexity

of natural systems (Berlow et al. 1999, Paine. 1980).

Although it has been argued that strong interactions can be negligible in assessing overall system impacts (Paine.1980), more studies are needed to parameterize environmental effects on prey selection (Barnes et al. 2010). Other studies have found water to dramatically and directly affect interactions of communities (McCluney. 2009)

The indirect effects of this study (Relaxed predation of the basal resource-Fi*G*.4) suggest that water may have a more direct influence on many system linkages and food web connectivity. Although predator mass and respective prey mass typically reflect a linear correlation leading to sized based trophic structuring (Barnes et al.2010), the role of water availability, especially at finer scales, may reveal predictable patterns of IGP, community structure and trophic dynamics, in terms of limitations and disturbances in water limited systems. Optimal foraging theory attempts to model and predict foraging behavior while the causes of foraging behavior may be less simple to quantify. Other studies have found nutrient limitation to have direct effects on reproductive and foraging behavior (Waldbauer & Friedman.1991). This study does not aim to quantify the intricacies of nutrient stoichiometry, nor the precise mechanism of dietary selection, in terms of nutrient balance, however there is evidence that free water availability has an influence on prey selection by *Hogna antelucana*. More studies are needed to determine precise thoracic lipid accumulations and if these prey selections effect the overall health and body composition of the wolf spiders.

Crickets at the onset of feeding, during the first and final larval stages exhibit lipids at 42% of fat body fresh mass (Anand & Lorenz.2008) and that a great amount of this stored energy reserve is carried over from the last larval stage, further augmented by

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voracious feeding to adult life for reproduction (Hill and Goldsworthy, 1968). Inversely, a study to determine prey selection of *Pardosa* sp. found that consumption was mediated by the previous feeding as spiders alter between protein or lipid rich flies to balance body nutrients (Mayntz el al. 2005). Although, different species of *Pardosa* have been found to express species specific variability of body compositions in regards to diet selection (Jensen et al. 2011), it can be assumed that *Pardosa* yield ratios of higher proteins to lipids than basal prey *Gryllus*.

Hogna antelucana, control nutrient balance and body composition by selecting for prey that are higher in energy to water ratios when water is abundant. This mechanism may translate in optimal body composition and prevent obesity. Trophic dynamics expressing IGP or cascades is based on the availability of prey and water. Thus, water and energy co-limited systems may have a greater degree of predatory shifting between IGP and interspecific competition in regards to trophic interactions mediated by water limitation alone.

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