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Predator water balance alters intraguild predation in a streamside food web

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Abstract. Previous work suggests that animal water balance can influence trophic interactions, with predators increasing their consumption of water-laden prey to meet water demands. But it is unclear how the need for water interacts with the need for energy to drive trophic interactions under shifting conditions. Using manipulative field experiments, we show that water balance influences the effects of top predators on prey with contrasting ratios of water and energy, altering the frequency of intraguild predation. Water-stressed top predators (large spiders) negatively affect water-laden basal prey (crickets), especially male prey with higher water content, whereas alleviation of water limitation causes top predators to switch to negatively affecting energy-rich midlevel predators (small spiders). Thus, the relative water and energy content of multiple prey, combined with the water demand of the top predator, influences trophic interactions in ways that can alter the strength of intraguild predation. These findings underscore the need for integration of multiresource approaches for understanding implications of global change for food webs.

Key words: Energetics; food webs; geometric framework; Gryllus; Hogna; hydration; intraguild predation; riparian; stoichiometry; water limitation.

Introduction

Food-web ecologists have historically focused on the role that energy plays in trophic interactions and food-web dynamics (Elton 1933, Lindeman 1942, Paine 1980, McCann 2011). More recently that view has been broadened by studies documenting the importance of nutrients and water in animal foraging decisions and food-web ecology (Sterner et al. 1996, Fagan et al. 2002, Sterner and Elser 2002, McCluney and Sabo 2009, 2016, Schmidt et al. 2012, Simpson and Raubenheimer 2012, Wilder et al. 2013, Allen et al. 2014, Deguines et al. 2017, McCluney 2017).

It is increasingly recognized that considering multiple limiting resources simultaneously can provide greater insight into species interactions than single-resource approaches (Sterner and Elser 2002, Simpson and Raubenheimer 2012). For instance, although contested (Wilder and Eubanks 2010), Denno and Fagan (2003) argued that mismatches in the nutritional requirements of predators and the nutritional content of prey could result in increased trophic omnivory and intraguild predation (IGP). More specifically, they suggested that nitrogen limitation by predators may drive increases in consumption of higher trophic levels (i.e., IGP), 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). Others have shown that predators may often be more limited by lipids than by nitrogen (Wilder et al. 2013), but the general idea that imbalances in resources influence foraging behavior, in ways that may alter intraguild predation, deserves further attention.

A number of studies have suggested or documented how animal water balance may influence foraging decisions, species interactions, and food webs (Noy-Meir 1974, Golightly and Ohmart 1984, Valeix et al. 2008, McCluney and Sabo 2009, 2016, McCluney et al. 2012, Allen et al. 2014). Generally, these studies show that when free water is limited, animals tend to consume more moist food (prey) in order to meet their water demand, which can greatly increase per-capita interaction strengths, and may alter entire food webs (reviewed in McCluney 2017). Therefore, water seems to have strong effects on trophic interactions, but relatively little is known about how water balance and availability of water, energy, or nutrients influences foraging decisions.

Here we hypothesize that predators switch between water-laden and energy-rich prey species depending on the relative strength of water and energy limitation
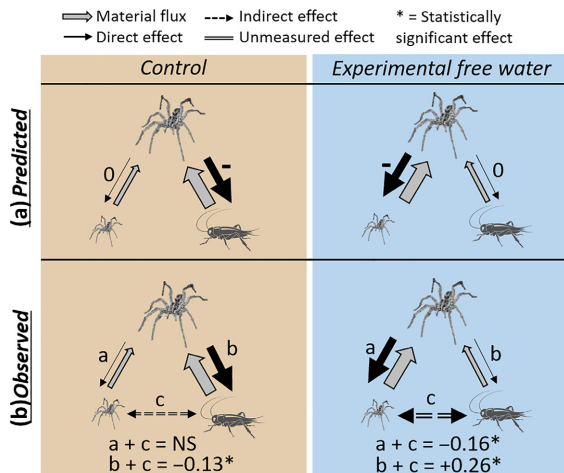
FIG. 1. Predicted and observed trophic relationships between the study taxa. Arrows are qualitative. Gray arrows represent fluxes of materials. Black arrows represent trophic effects, with dashed double-line arrows representing unmeasured indirect effects. Quantitative effect sizes are written at the bottom for the combination of direct and indirect effects (labeled a, b, and c), because these cannot be separated in this study. Asterisks denote statistically significant effects. Large spiders had stronger negative effects on crickets under dry conditions, but stronger negative effects on small spiders under moist conditions.

(Fig. 1). We explore this hypothesis within the context of omnivory and intraguild predation. Specifically, we hypothesize that top invertebrate predators (here, large wolf spiders) select water-laden prey when they are water stressed, but eat prey with higher relative energy content when water stress is experimentally reduced. We explore these questions in experimental mesocosms involving top predators (here, large spiders), primary consumers (here, crickets), and intraguild predators (here, smaller spiders) that we predict will vary in relative water and energy content based on previous measurements (Sabo et al. 2008) and differing demands expected from life history. For instance, we expect that female and male predators should be subject to different energetic constraints because of costs of reproduction—female egg production and reproductive behavior vs. male competition for mates. Thus, we predict that female top predators will show stronger IGP across water treatments than males, to because of higher energetic costs associated with gamete production and provisioning to offspring. Moreover, we hypothesize that water stress will drive top predators to eat more male prey, because these males should have higher relative content than females of the same species (because of egg production by females).

METHODS

Study site and species

The experiment took place in the semiarid floodplain forest of the San Pedro River in Southeast Arizona, during low-flow conditions. The San Pedro is one of the last undammed rivers in the southwestern United States, originating in northern Mexico and traveling north until joining with the Gila River, a tributary of the Colorado River. The river has a highly variable hydrograph with major flooding in the monsoon season (late June to September), but with floodplain soils with low soil moisture in the early summer dry season (Sabo et al. 2008, McCluney and Sabo 2016). The floodplain is characterized by an overstory of cottonwood (*Populus fremontii*) and willow trees (*Salix* sp.). Boasting over 250 breeding bird species and 80 species of mammals, the river is among the most ecologically diverse in the United States (Stromberg and Tellmann 2009).

Experiments were conducted during the dry season (from May 2 to July 6, 2012) in a floodplain forest with an overstory of cottonwood trees, approximately 30% small to medium dry grasses, and a sandy loam soil matrix. Daytime temperatures during this period ranged from 27° to 37°C, with the mean peak temperature at 35°C. Night temperatures ranged from 15° to 21°C, with a mean low of 18.6°C. Soil moisture was very low in the experimental area, ranging from 3 to 12% by volume, and there were no rainfall events during the trials. Thus, water sources outside of mesocosms were limited to water obtained from food and water from moist soils near the flowing river. Within mesocosms, consumers did not have access to moist soil.

Our lab and field experiments involved common species used in previous studies (McCluney and Sabo 2009): a top invertebrate predator, the large wolf spider *Hogna antelucana*, intermediate invertebrate predators, smaller wolf spiders, including *Pardosa* sp., and a basal consumer, the damp-loving field cricket, *Gryllus alogus*. The large wolf spiders used here have been documented consuming both crickets and small spiders outside of mesocosms. However, we have not observed the small spiders consuming the adult field crickets we used in these experiments. The adult crickets used here were ~20× the mass of the small spiders on average (100 vs. 5 mg dry mass). Even the smallest measured cricket was ~8× larger than the largest measured Pardosa, by mass. Thus, although we cannot completely rule out the possibility of a small spider consuming a cricket, small spiders are unlikely to be efficient predators of these adult crickets.

Laboratory measurement of prey water and energy content

Gravimetric water content.—We used gravimetric methods to quantify water content of arthropod prey and predators. Arthropods were collected in the evening, adjacent to experimental mesocosms, and frozen in pre-weighed glass polyseal vials within 1 h of capture. Thus, our measurements are of field water content of animals outside cages. Six samples (free of defect, lost limbs) of each species were processed. All animals frozen for gravimetric measurement were dried to a constant mass at 65°C for a minimum of 12 h. Dry masses were re-weighed for calculations and redried in preparation for bomb calorimeter protocols.

Calorimetry.—We used bomb calorimetry to determine total energy content (J) of arthropod predators and prey. Dry masses of field spiders previously evaluated for water content by gravimetric procedures were prepared individually into pellets of approximately 50 mg at time of calorimeter sampling. Samples were placed within a large desiccator to prevent ambient rehydration. Calorimetry was achieved using a Parr model 1425 Semimicro Calorimeter standardized using benzoic acid pellets. All samples and standards were run in double and averaged to reduce machine bias/error. The unexpired fuse from samples was weighed to correct calculations. One hundred percent oxygen was used to fire the fuse, and room temperature distilled water was used to encase the bomb. The electrodes that sparked the fuse were brushed clean prior to each sample run. Fuse wire was No. 45C10 at 2.3 cal/cm.

Bomb calorimetry does not provide a direct estimate of metabolizable energy because exoskeleton material is included in energy content estimates from bomb calorimetry, but is indigestible for many consumers. However, we note that the exoskeleton content of our taxa is relatively low compared to some other taxa (e.g., beetles; Evans and Sanson 2005). But because crickets have higher exoskeleton content than spiders, biases could exist. Specifically, measures using bomb calorimetry should overestimate the energy content of crickets relative to spiders. Thus, our use of bomb calorimetry should only be a potential problem if the estimated energy content of crickets appears greater than spiders. This did not appear to be the case (see Results).

Standardization of masses.—We standardized water or energy contents (and their ratio) to the mean water content of either female or male *Hogna* (putative top predators), setting the target predator content to one. This standardization allows for direct comparison of the water (g) or energy (J) content of prey relative to that of predators. However, we also report raw estimates of water and energy content.

Field experiment to compare interaction strength of intraguild predators

To quantify the effects of free water availability on relative interaction strengths and IGP in this arthropod community, we designed and executed a field experiment in which we experimentally manipulated water availability (two levels: free water added or not added) and community composition (Table 1). Community composition treatments were achieved by modifying the presence/absence of male/female top predators (large spiders) and the presence of male vs. female basal prey (field crickets) in a factorial design, but with intermediate predators (small spiders) always present. To calculate per-capita interaction strengths between top predators and intermediate predators and basal prey, we compared cages with top predators to controls without top predators.

TABLE 1. Treatments and sample size for field experiment examining effects of water supplementation, community structure, and sex of predators and prey on interaction strength of intraguild predators on intermediate predators and on prey.

Community	top predator† →	Present				Absent
	top predator sex→	♀	♀	♂	♂	NA
	basal prey sex→	♀	♂	♀	♂	♀ and ♂
Free water	present	9	7	7	6	7
	absent	5	8	8	9	6

† All treatments included ambient densities of intermediate predators.

Controls (six with, six without free water) consisted of cages without top predators but with intermediate predators and equal numbers of male and female basal prey (crickets) present (density matched to treatments).

To do this, we assembled enclosures (2 × 2 × 2 m in dimension), removed all spiders and crickets, and added back these animals to match target densities (Table 1). We manipulated water availability using Zilla© water pillows which hold ~30 mL of free water (described in McCluney and Sabo 2009, 2016). This method has been shown to increase the water content of arthropods in the field (McCluney et al. 2018). Although we did not measure how the water content of animals within the experimental mesocosms changed over time (requires destructive sampling), we expect diurnal variation in water content occurred, as well as variation over time as the experiment progressed. However, on average, all arthropods in the water-added treatments should have had a higher hydration than in the dry ambient treatments, although crickets should have been less affected due to the presence of moist leaves, supplied daily, in all treatments.

We assembled eight enclosures in each of three areas (not more than 10 m apart) in an area between 5 and 30 m 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, Allen et al. 2014). Enclosures consisted of a fitted 240-micron mesh cover, placed over §-inch (1.19 cm) PVC frames. Each cage had a door for re-entry that sealed with hot-glued Velcro strips. The base of the PVC, with the mesh attached (wrapped and zip tied), was buried ≤25 cm deep in surrounding soil.

We prepped enclosures by removing cottonwood leaf litter from all cages and then restocking to a constant depth of 4–5 cm. All arthropods were also removed and litter was sun dried between two thermoreflective silver tarps (minimum drying temperature 60°C). Close inspections revealed that all leaves were void of arthropods. In addition to rationed leaf litter, we stocked each cage with standardized refuge—a 20 × 30 × 3.75 cm, flat, non-painted piece of lumber (fir), used as a proxy of large woody debris common in the understory, and used frequently by arthropods as refuge from midday heat. We fed field crickets a daily ration of two fresh cottonwood

leaves from a pool of freshly picked leaves of similar size (±2 cm) and chlorophyll quality estimated by coloration.

We executed our experiment in three temporally distinct trials in which treatments (and controls) were approximately equally distributed (not counting failed replicates; see Table 1). In each trial, half of the enclosures were randomly designated for water supplementation and received a single water pillow. Water pillows were replaced every 24 h. Water pillows were hydrated using water collected daily from clear water areas of the San Pedro River.

The night prior to the experiment, we hand-collected 36 large wolf spiders, *H. antelucana*, (54 small wolf spiders, *Pardosa* sp., and 60 field crickets, *G. alogus*, at sites along the river >100 m from enclosure sites. Spiders were kept isolated to prevent attack, damage, or unnecessary stress. From each collection, six of each species were weighed in preweighed polyseal vials and frozen for future gravimetric studies. The remaining spiders and prey were marked with fluorescent acrylic paint markers for easy re-location and identification (sex) and used in the trials.

We added a single large spider, *H. antelucana* (male/female per treatment), to all of the cages except those serving as controls. We then added two small spiders, *Pardosa* sp., and two field crickets, *G. alogus* (adult male/female per treatment). We determined the appropriate number of prey based on previous research. In McCluney and Sabo (2009), spiders consumed a mean of 0.016 crickets per day when water was added and 0.16 crickets per day in the dry cages. Thus, for our 4-day trials, spiders could have been expected to consume the equivalent of 6–64% of a single cricket, less than the stocking density here. Sabo et al. (2008) reported a mean ambient cricket density of two crickets per square meter ,whereas we stocked cages to a density of one per square meter. Thus, in this study, densities were lower than ambient, but sufficient to meet energy and water demands.

In this experiment, we relied on controls that were free of top predators (*H. antelucana*) to differentiate predation from natural ("background") mortality. Control cages were free of top predators but had all possible prey, including two small spiders, and two male and two female field crickets (four total). Trials were continued for 96–100 h, at which time we surveyed predator and prey abundances to estimate interaction strengths.

At the end of each trial, we identified and captured all living experimental subjects. We used UV flashlights to help find individuals, which were painted with fluorescent paint. When we found the painted remains of a dead individual, we recorded mortality as a full individual, whereas when we simply could not relocate the individual, we recorded mortality as half (0.5) an individual. The consistency of leaf litter and wood structure also made the timed searches effective. Searches were timed at 15 min per cage and a team of four took ~90 min to complete each survey. Cages were also inspected by day for intruders, and occasional diurnal arthropods were

identified and removed. Invasion by these nontarget species was very low (13 nonmarked intruder individuals were found and removed across all cages and trials; taxa included juvenile crickets, a funnel weaver spider, and a wasp). Each of the 10 treatment combinations had 5–9 replicates (including controls; $N = 72$) in sets of three experimental trials. Thus, we attempted to balance the design, but failure of some replicates made the results unbalanced.

Estimation of interaction strengths

Dynamic interaction strengths were estimated following (Wootton 1997, Berlow et al. 1999)

$$\alpha = \frac{-\ln\left(\frac{R_{NoC}}{R_C}\right)}{C} \quad (1)$$

where α is per-capita interaction strength, R_{NoC} is resource abundance in the top predator removal enclosure (NoC), R_C is resource abundance (either small spiders or crickets) in the experimental enclosure (with top consumer, C), and C is density of the top consumer (here always unity, by definition based on treatment). Logistical constraints prevented us from pairing control enclosures ($n = 13$; 6 no water, 7 water) with each experimental enclosure ($n = 61$). Hence, we used mean control resource abundance ($\bar{R}_C$ in water or no-water treatments) instead of paired control abundance to correct predation estimates for background mortality.

Data analysis

We analyzed differences in interaction strength using linear mixed models with water (presence/absence) and top predator (large spiders) and basal prey (crickets) sex (male/female) as fixed effects and temporal trials as random effects using the lme function within the R programming language. We assessed data for normality and equal variance using normal probability plots (quantile–quantile [Q–Q]) and residual plots. Interaction strength data met the equal variance assumption, but were moderately nonnormal; hence, we proceeded with analysis of untransformed data, because ANOVA is somewhat robust to violations of the normality assumption.

RESULTS

Water and energy content of resources

Total field energy and water content was highest for female large spiders, *H. antelucana* (Figure 2; Table 2; raw data can be found in Data S1: WaterContent.csv, EnergyContent.csv, and StandardizedEnergyWater.csv). Total energy content of female large spiders was more than twofold higher than male large spiders and small spiders (*Pardosa*). Small spider energy content was
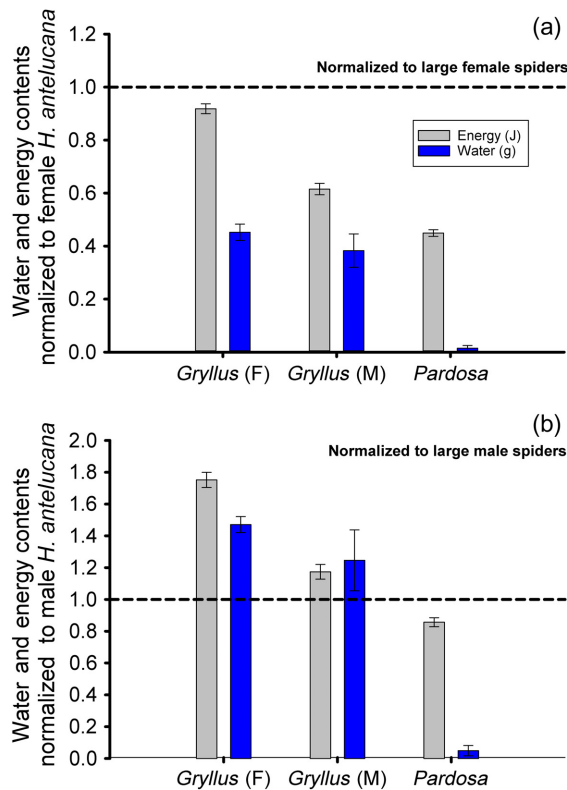
Fig. 2. Total field energy (J) and water (g) contents of prey species, standardized to male and female large spiders (content of large spiders indicated by dashed line at 1). (a) Female and (b) male large spiders (*Hogna antelucana*). Gravimetric methods used to determine total water content (g) and bomb calorimetry to derive total energy (J) content. Because of the standardization, results are unitless ratios rather than joules or grams. Note: Female spiders and crickets used in the study are sexually mature gravid specimens.

~1.67-fold higher than male crickets (*G. alogus*) but was on par (<10% higher) with female crickets. Water content of female large spiders was more than twofold higher than male and female crickets, and more than 10-fold higher than small spiders. Interestingly, male large spiders had lower water content relative to females (Fig. 2) and, hence, much higher energy relative to water

content than females. Small spiders had the lowest energy content of all resources, but even lower water content (Fig. 2); thus, the energy-to-water ratio of small spiders is >30-fold higher than female large spiders (Fig. 3) and the highest of all prey species (including crickets). Unstandardized water and energy content of each individual of each taxa and sex can be found in Data S1: WaterContent.csv and EnergyContent.csv.

Intraguild predation and experimental interaction strengths

Experimental additions of free water via water pillows significantly changed the effects of large spiders on lower trophic levels, leading to higher per-capita predation on small spiders (i.e., greater IGP; Fig. 4a; Fig. 1, Table 3; raw data can be found in Data S1: AbundIS.csv) and weaker predation on crickets (Fig. 4b, Fig. 1, Table 3). This result did not differ between male and female large spiders (Fig. 4a, Table 3). Addition of water led to *positive* per-capita effects of large spiders on crickets (Fig. 4b, Table 3). This effect was stronger on male than female crickets. We note that mean survival of all prey items in no-predator control cages was 67.9% in water-added treatments and 69.4% in dry cages, whereas in predator cages, survival was 17.2% in water-added treatments and 12.9% in dry cages (see Data S1: AbundIS.csv for raw data).

DISCUSSION

Here we show that water demand and the relative energy : water content of prey appears to drive top-down effects of predators on intraguild prey and primary consumers. Specifically, large spiders switch between killing high-water-content crickets and high-energy-content small spiders in response to experimental manipulation of free water. Alleviation of water stress precipitates stronger intraguild predation and release of predation pressure on primary consumers. Surprisingly, these differences do not vary between treatments with male or female top predators (large spiders), in spite of potentially higher energy demand by reproductive females. Although there was no significant difference

TABLE 2. Mean and ± standard error of dry mass (g), total field energy content (J), and total field water content (g) of each organism in the study, not standardized to the predator.

Organism	Sex	Mean dry mass (g)	Mean energy (J)	Mean water (g)	Mean energy:mean water
Large spider	F	0.1768 ± 0.0206	2.1014 ± 0.0260	0.3164 ± 0.0209	6.6426
Large spider	M	0.0566 ± 0.0023	1.1014 ± 0.0245	0.0972 ± 0.0027	11.3336
Cricket	F	0.1205 ± 0.0071	1.9298 ± 0.0308	0.1430 ± 0.0275	13.4988
Cricket	M	0.0809 ± 0.0091	1.2932 ± 0.0421	0.1211 ± 0.0183	10.6788
Small spider	NA	0.0050 ± 0.0006	0.9438 ± 0.0238†	0.0048 ± 0.0026	198.8398

Note: Values are based on six individuals, unless noted. Raw values for each individual are available in the supplementary information.

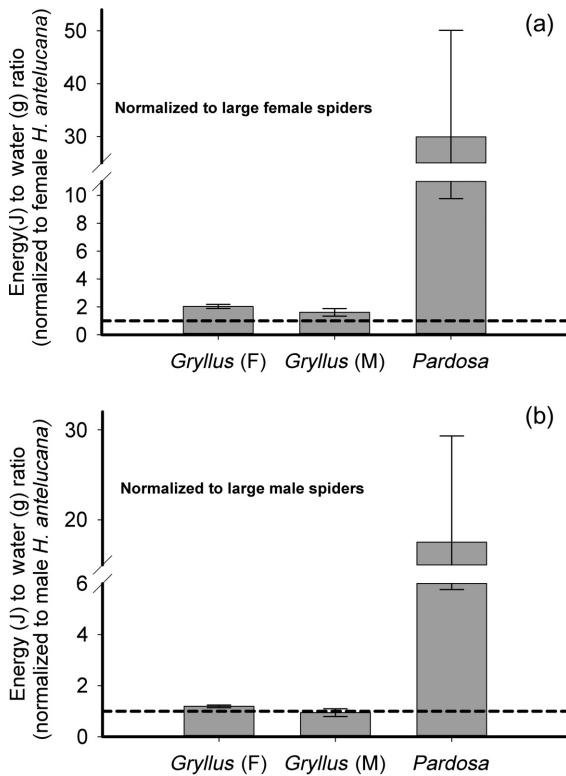† Energy content of small spiders based on four individuals.

FIG. 3. Comparative ratios of mean total energy (J) to water (g), standardized to male and female large spiders (ratio for large spiders indicated by dashed line at 1). (a) Female and (b) male large spiders (*H. antelucana*). Note that the intermediate predator provides 100-fold the total energy content of all other prey, relative to total water content.

between the effects of male and female large spiders on small spiders, the indirect effects of large spiders were more strongly positive on male crickets than female crickets. Hence, free water has effects on primary consumers (release), but the effect varies depending on the sex of the primary consumers. In sum, these results suggest that energy and water combine to influence trophic dynamics in this desert riparian food web. Importantly, these effects are at least partially predictable based on measured differences in water and energy content among prey.

Water-mediated IGP and indirect effects

The top predator in our system (large spiders) appears to seek water by choosing prey with the highest water content (crickets) and appears to switch to intermediate predators when free water is supplemented. These intermediate predators have between 6- and 30-fold higher energy : water ratios relative to male and female large spiders, respectively. The impact of switching on prey population dynamics has a well-documented history in population and community ecology (Murdoch 1969, Murdoch and Stewart-Oaten 1975). More recent
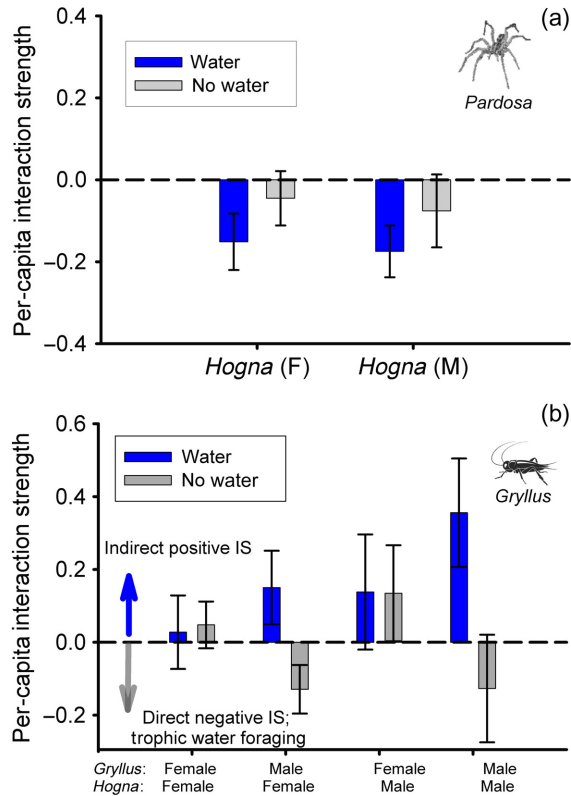

FIG. 4. (a) Interaction strength (IS) between the top predator, a large spider (*H. antelucana*) and the intermediate predator, a small spider (*Pardosa* sp.). Negative effects on small spiders increase with free available water regardless of respective sex. (b) Interactions between the top predator, a large spider (*H. antelucana*), and the primary consumers (crickets, *G ryllus alogus*).

TABLE 3. Results from linear mixed-effects analysis of effects of water and predator and prey sex on intraguild predators (small spiders, *Pardosa* sp.) and basal prey (*Gryllus alogus*).

Effect	df	SS	MS	F	P
Small spiders (*Pardosa*)					
Water	1	0.15	0.15	6.44	**0.014**
Top predator sex	1	0.01	0.01	0.48	0.493
Prey sex	1	0.00	0.00	0.17	0.679
Water:predator sex	1	0.00	0.00	0.01	0.908
Water:prey sex	1	0.00	0.00	0.02	0.875
Predator sex:prey sex	1	0.00	0.00	0.05	0.822
Water:predator sex:prey sex	1	0.05	0.05	2.39	0.128
Error	51	1.15	0.02		
Crickets (*Gryllus alogus*)					
Water	1	0.48	0.48	8.18	**0.006**
Predator sex	1	0.17	0.17	2.82	0.099
Prey sex	1	0.01	0.01	0.21	0.647
Water:predator sex	1	0.04	0.04	0.66	0.420
Water:prey sex	1	0.56	0.56	9.46	**0.003**
Predator sex:prey sex	1	0.00	0.00	0.00	0.969
Water: predator sex:prey sex	1	0.03	0.03	0.49	0.487
Residuals	51	2.99	0.05		

Bold values indicate statistical significance at $\alpha = 0.05$.

research broadens the notion of switching in the context of intraguild predation (Fagan et al. 2002, Denno and Fagan 2003). Specifically, this newer view suggests that nitrogen-limited predators will eat higher on the food web—engaging in IGP—in pursuit of prey with higher protein and, hence, lower C : N ratios (although others argue that lipids are more limiting at higher trophic levels; Wilder et al. 2013). Our results provide support for this idea in the context of water and energy (sensu Noy-Meir 1973, 1974)—top predators engage in IGP on energy-rich intraguild predators, but only when relieved from water stress.

In addition to the strong negative, direct effects of large spiders on small spiders with water, or on crickets without free water, large spiders had significant positive effects (rather than neutral) on crickets with water. The exact mechanism behind this effect is unclear. One possible explanation for this effect is fear of predation. When large spiders killed more small spiders with added water, this could have lowered overall spider density, decreasing or altering the type of predator cues detected by crickets (large spider odor cues could reflect recent predation on small spiders instead of recent predation on crickets; Persons et al. 2001). Lower fear of predation by crickets could have led to changes in cricket behavior (Storm and Lima 2008) that increased survival (e.g., more time consuming moist leaves or more time drinking from water pillows and less time hiding). This represents just one possible explanation for the observed pattern and more work is needed to understand potential mechanisms for this positive (rather than neutral) effect of large spiders on crickets when water was added. Regardless, our results suggest that water alters rates of intraguild predation, with added water releasing crickets from predation pressure, but increasing predation pressure on small spiders.

Other possible mechanisms

We note there are several alternative potential mechanisms that could help explain our observed results. First, we note that although small spiders had a higher relative energy content than crickets, because crickets are larger, they had more total energy; thus, one might expect large spiders to always consume crickets, meeting both water and energy needs. However, we do see stronger negative effects of large spiders on small spiders with added water, suggesting a trade-off between consumption of crickets and small spiders exists. One possible mechanism behind this observation is that spider gut limitation prevents consuming an entire adult cricket. Thus, given limited ingestion potential and adequate environmental hydration, it is better to consume the small spider, which has higher relative energy content, than to attempt to consume a cricket, in which energy is more dilute.

Alternatively, the possibility exists that the observed results are driven by a trade-off between water demand and risk to the top predator (sensu Mayntz and Toft 2006) and are not related to energy content of the prey.

It may be more difficult or risky for a large spider to catch an adult cricket than a small spider. When water is limited, the hydration benefit of consuming a water-laden cricket may outweigh the difficulty or risk, but when environmental water is provided, it may be easier or safer to consume a small spider.

Changes in consumer behavior could also potentially be involved in the response. If the presence of water pillows attracts both the predator and prey into closer contact, the frequency of predation might increase (sensu Valeix et al. 2008). But we are uncertain of a reason to expect that small spiders would be more greatly attracted to water pillows than would crickets. Both taxa have been commonly observed using water pillows in other experiments outside cages (Allen et al. 2014, McCluney and Sabo 2016). Additionally, predation events have not been observed on water pillows outside cages in this area, but predation events have been commonly observed without water pillows. However, we cannot rule out the possibility that greater attraction of small spiders to water pillows, than crickets, is responsible for the increased negative effect of large spiders on small spiders with added water.

Another change in predator or prey behavior—increased activity in response to water pillows—could also potentially help explain our results. For instance, gila monsters increase their foraging activities in response to water supplementation (Davis and DeNardo 2009). If water stimulated foraging activity, one would expect an increase in per-capita predation overall, but McCluney and Sabo (2009) found a substantial decrease in predation with water supplementation, using a similar setup involving the same taxa of large spiders and crickets (but no small spiders). Thus, although we cannot exclude the possibility that changes in activity of prey or generalized foraging activity of the large predators could influence the observed results, we discount this possibility.

Overall, multiple behavioral mechanisms may be involved in producing the switch in predation from crickets to small spiders with water supplementation. Additional research into the effects of water on the behavioral ecology of these and other species is warranted.

Sexual dimorphism IGP impacts

Differences in the sex of the top predator did not alter the effects of the top predator (Fig. 4). This was a surprise, given that we expected female spiders to have higher energy demands related to egg production (Givens 1978). In contrast to consistent effects of different sexes of large predators, effects differed between sexes of crickets. Free water enhanced survival (i.e., positive interaction strength) of male crickets only. We offer two potential mechanisms for this difference: (1) intersexual differences in energy : water ratios of crickets, or (2) an intersexual difference in prey detectability. Male crickets were more water-laden than female crickets (Fig. 3); hence with free water

supplementation, the difference between the energy&hairsp: water content of crickets and small spiders was larger for male crickets, leading to stronger trade-offs and stronger switches to consumption of small spiders. Alternatively, it could be that male crickets are generally more detectable than female, and thus, the first measurable impact of free water is on these easily targeted prey. Male crickets create vibrations when producing their mating calls via stridulation (Robinson and Hall 2002) and mate calling may have contributed to higher detectability of male crickets (Zuk and Kolluru 1998).

IGP in a water-web context

Our observation that the strength of IGP varied with water availability is important. Intraguild predation has been shown, both in theory in practice, to have strong impacts on population dynamics and trophic structure (Polis and Holt 1992, Wissinger and McGrady 1993, Holt and Polis 1997, Sih et al. 1998, Wise and Chen 1999, Finke and Denno 2004). Specifically, increased IGP can dampen trophic cascades (Bascompte et al. 2005) and enhance community stability (Polis and Strong 1996, Fagan 1997). In the desert riparian food web at the San Pedro River studied here, decreases in water availability may strengthen the potential for trophic cascades via three mechanisms: (1) inducing a strong numerical response of multiple trophic levels (including large spiders; Allen et al. 2014), (2) increasing interaction strengths between predators and basal consumers and between basal consumers and plants (McCluney and Sabo 2009, 2016), and (3) reducing IGP (documented here).

Our results help provide evidence for a mechanism behind the pattern observed in a separate large-scale, open-air manipulative food-web study conducted at a nearby location along this river (McCluney and Sabo 2016). In that study, large top predators (also the large spider *H. antelucana*) and water availability were also manipulated, and the effects of large spiders on smaller spiders (*Pardosa* spp. and others) also varied with water availability, but the authors were unable to determine a mechanism. Here, we show that water supplementation increases predation on small spiders, which is consistent with the pattern observed in the open-air experiment. Thus, although our experiment involves short-term manipulations of simplified food webs in cages, our results may describe processes that can occur in more complex food webs (sensu McCann 2011).

Although we directly only investigated how relative water and energy content influence predation, we believe our research also has relevance for understanding nutritional ecology. Many studies have now shown how animals may forage from multiple foods of varying nutrient content to meet their target ratios of nutrient intake (Simpson and Raubenheimer 2012). In one particularly relevant example, wolf spider (*Pardosa*) prey selection was modified by the previous feeding, with spiders switching between protein or lipid-rich flies to balance body nutrients (Mayntz et al. 2005). Here we show that spiders may also be similarly balancing water and energy intake and that this has effects on species interactions and food webs.

LITERATURE CITED

Allen, D. C., K. E. McCluney, S. R. Elser, and J. L. Sabo. 2014. Water as a trophic currency in dryland food webs. Frontiers in Ecology and the Environment 12:156–160.

Bascompte, J., C. J. Melian, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. Proceedings of the National Academy of Sciences USA 102:5443–5447.

Berlow, E. L., S. A. Navarrete, C. J. Briggs, M. E. Power, and B. A. Menge. 1999. Quantifying variation in the strengths of species interactions. Ecology 80:2206–2224.

Davis, J. R., and D. F. DeNardo. 2009. Water supplementation affects the behavioral and physiological ecology of Gila Monsters (*Heloderma suspectum*) in the Sonoran Desert. Physiological and Biochemical Zoology 82:739–748.

Deguines, N., J. S. Brashares, and L. R. Prugh. 2017. Precipitation alters interactions in a grassland ecological community. Journal of Animal Ecology 86:262–272.

Denno, R. F., and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? Ecology 84:2522–2531.

Elton, C. 1933. The ecology of animals. Methuen, London, United Kingdom.

Evans, A. R., and G. D. Sanson. 2005. Biomechanical properties of insects in relation to insectivory: cuticle thickness as an indicator of insect "ardness" and "intractability." Australian Journal of Zoology 53:9–19.

Fagan, W. F. 1997. Omnivory as a stabilizing feature of natural communities. American Naturalist 150:554–567.

Fagan, W. F., and R. F. Denno. 2004. Stoichiometry of actual vs. potential predator–prey interactions: insights into nitrogen limitation for arthropod predators. Ecology Letters 7:876–883.

Fagan, W. F., E. Siemann, C. Mitter, R. F. Denno, A. F. Huberty, H. A. Woods, and J. J. Elser. 2002. Nitrogen in insects: implications for trophic complexity and species diversification. American Naturalist 160:784–802.

Finke, D. L., and R. F. Denno. 2004. Predator diversity dampens trophic cascades. Nature 429:407–410.

Givens, R. P. 1978. Dimorphic foraging strategies of a salticid spider (*Phidippus audax*). Ecology 59:309–321.

Golightly, R. T., and R. D. Ohmart. 1984. Water economy of two desert canids—coyote and kit fox. Journal of Mammalogy 65:51–58.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist 149:745–764.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–418.

Mayntz, D., D. Raubenheimer, M. Salomon, S. Toft, and S. J. Simpson. 2005. Nutrient-specific foraging in invertebrate predators. Science 307:111–113.

Mayntz, D., and S. Toft. 2006. Nutritional value of cannibalism and the role of starvation and nutrient imbalance for cannibalistic tendencies in a generalist predator. Journal of Animal Ecology 75:288–297.

McCann, K. S. 2011. Food webs (MPB-50). Princeton University Press, Princeton, New Jersey, USA.

McCluney, K. E. 2017. Implications of animal water balance for terrestrial food webs. Current Opinion in Insect Science 23:13–21.

McCluney, K. E., J. Belnap, S. L. Collins, A. L. Gonzalez, E. M. Hagen, J. Nathaniel Holland, B. P. Kotler, F. T. Maestre, S. D. Smith, and B. O. Wolf. 2012. Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. Biological Reviews of the Cambridge Philosophical Society 87:563–582.

McCluney, K. E., T. George, and S. D. Frank. 2018. Water availability influences arthropod water demand, hydration and community composition on urban trees. Journal of Urban Ecology. https://doi.org/10.1093/jue/juy003

McCluney, K. E., and J. L. Sabo. 2009. Water availability directly determines per capita consumption at two trophic levels. Ecology 90:1463–1469.

McCluney, K. E., and J. L. Sabo. 2016. Animal water balance drives top-down effects in a riparian forest—implications for terrestrial trophic cascades. Proceedings of the Royal Society B 283:20160881.

Murdoch, W. W. 1969. Switching in general predators. Experiments on predator specificity and stability of prey populations. Ecological Monographs. https://doi.org/10.2307/1942352

Murdoch, W. W., and A. Stewart-Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:1–131.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Noy-Meir, I. 1974. Desert ecosystems: higher trophic levels. Annual Review of Ecology and Systematics 5:195–214.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:666–685.

Persons, M. H., S. E. Walker, A. L. Rypstra, and S. D. Marshall. 2001. Wolf spider predator avoidance tactics and survival in the presence of diet-associated predator cues (Araneae: Lycosidae). Animal Behaviour 61:43–51.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology & Evolution 7:151–154.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147:813–846.

Robinson, D. J., and M. J. Hall. 2002. Sound signaling in orthoptera. Pages 151–278 in A. Evans, editor. Advances in insect physiology. Volume 29. Elsevier, Amsterdam, Netherlands

Sabo, J. L., K. E. McCluney, A. C. Keller, Y. Y. Marusenko, and C. U. Soykan. 2008. Greenfall links groundwater to aboveground food webs in desert river floodplains. Ecological Monographs 78:615–631.

Schmidt, J. M., P. Sebastian, S. M. Wilder, and A. L. Rypstra. 2012. The nutritional content of prey affects the foraging of a generalist arthropod predator. PLoS ONE 7:e49223.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution 13:350–355.

Simpson, S. J., and D. Raubenheimer. 2012. The nature of nutrition: a unifying framework from animal adaptation to human obesity. Princeton University Press, Princeton, New Jersey, USA.

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, New Jersey, USA.

Sterner, R. W., J. J. Elser, T. H. Chrzanowski, J. H. Schampel, and N. B. George. 1996. Biogeochemistry and trophic ecology: a new food web diagram. Pages 72–80 in G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman & Hall, New York, New York, USA.

Storm, J. J., and S. L. Lima. 2008. Predator-naive fall field crickets respond to the chemical cues of wolf spiders. Canadian Journal of Zoology 86:1259–1263.

Stromberg, J. C., and B. Tellmann. 2009. Ecology and conservation of the San Pedro River. University of Arizona Press, Tucson, Arizona, USA.

Valeix, M., H. Fritz, R. Matsika, F. Matsvimbo, and H. Madzikanda. 2008. The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. African Journal of Ecology 46:402–410.

Wilder, S. M., and M. D. Eubanks. 2010. Might nitrogen limitation promote omnivory among carnivorous arthropods? Comment. Ecology 91:3114–3117.

Wilder, S. M., M. Norris, R. W. Lee, D. Raubenheimer, and S. J. Simpson. 2013. Arthropod food webs become increasingly lipid-limited at higher trophic levels. Ecology Letters 16:895–902.

Wise, D. H., and B. R. Chen. 1999. Impact of intraguild predators on survival of a forest-floor wolf spider. Oecologia 121:129–137.

Wissinger, S., and J. McGrady. 1993. Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. Ecology 74:207–218.

Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: Diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67:45–64.

Zuk, M., and G. R. Kolluru. 1998. Exploitation of sexual signals by predators and parasitoids. Quarterly Review of Biology 73:415–438.

Supporting Information