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Water availability directly determines per capita consumption at two trophic levels

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Abstract. Community ecology has long focused on energy and nutrients as currencies of species interactions. Evidence from physiological ecology and recent studies suggest that in terrestrial systems, water may influence animal behavior and global patterns of species richness. Despite these observations, water has received little attention as a currency directly influencing animal species interactions. Here, we show that the per capita interaction strength between predatory wolf spiders and their primary prey, field crickets, is strong (-0.266) when predators and prey are maintained in ambient dry conditions, but is near zero (0.001) when water is provided ad libitum. Moreover, crickets consume 31-fold more moist leaf material in ambient dry conditions, switching from old litter to moist green leaves when free water is scarce. Under dry conditions, animals may make foraging decisions based first on water needs, not energy or nutrients, suggesting strong and predictable effects of alterations in aridity on species interactions.

Key words: climate change; per capita interaction strength; physiological ecology; water availability; water web.

INTRODUCTION

Understanding the environmental determinants of animal behavior and trophic interactions is key to efforts to predict the impacts of climate change on biodiversity (Sanford 1999, Helmuth et al. 2005, Suttle et al. 2007) and to aid efforts for ecological sustainability (Navarrete et al. 2005). Food web ecologists have long focused on energy as a currency for species interactions (Elton 1933, Lindeman 1942, Deruiter et al. 1995, Brown et al. 2004). In dry environments, which comprise one-third of earth's land mass (Schlesinger et al. 1990), and in all terrestrial systems during droughts, water limitation drives ecosystem processes, plant species composition, and animal consumption behavior (Noy-Meir 1973, Golightly and Ohmart 1984, Huxman et al. 2004). This insight is not new to organismal or single species-based approaches to biology. For example, animal physiologists have long recognized the fundamental importance of water as a resource (Noy-Meir 1974, Cooper 1985, Wolf and Walsberg 1996). In a community context, Noy-Meir (1973, 1974) postulated that arid regions are limited more by water than energy, such that arid ecosystems may best be represented by conceptual models using water as a currency instead of energy (i.e., a water web; Sabo et al. 2008). However, since then, animal community ecologists have done little to investigate water's influence on interactions (but see

Preisser and Strong 2004, Lensing and Wise 2006, Spiller and Schoener 2008). Greater interest in the effects of water limitation on animal communities is warranted considering recent work that suggests, at broad geographic scales, both plant and animal species richness patterns are correlated with water variables more than energy, at all but the most northern latitudes globally (Hawkins et al. 2003).

We examined the role of water as the currency for species interactions between a predator (the wolf spider, *Hogna antelucana*) and its primary prey species (the field cricket, *Gryllus alogus*), and per capita consumption of fresh green leaves (simulating greenfall) by crickets, in a semiarid riparian (streamside) forest along the San Pedro River in Arizona, USA. This river has extremely high bird, mammal, and reptile richness (Glennon 2002) and has been experiencing increasingly frequent drying events (McKinnon 2007) that lead to surface water scarcity for riparian animals. The impacts of drying events on terrestrial animal communities in this system and other similar desert riparian systems are unknown.

Two key observations guided our work and informed our hypotheses. First, most physiological models of animal water balance (e.g., Hadley 1994) indicate that when free water intake decreases (e.g., next to a drying river or during drought), an animal must respond with increased consumption of moist food or decreased water losses, or the animal will suffer dehydration. Conversely, an increase in free water (when initial conditions are dry) may lead to a decrease in consumption of moist food (all else being equal), or may allow for increased water losses (e.g., associated with increased movement). Second, we

Manuscript received 3 September 2008; revised 1 December 2008; accepted 19 December 2008; final version received 14 January 2009. Corresponding Editor: D. H. Wise.

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relied on evidence from the same study system that strongly indicates crickets are water limited during the dry summer months and seek to ameliorate this limitation by consuming greenfall (Sabo et al. 2008). Thus, we hypothesized that the availability of free water (for direct consumption) would have a significant influence on the consumption behavior of spiders and thus trophic interaction between crickets and spiders and on per capita consumption of green leaves by crickets.

Effects of water on trophic interactions may occur via alteration of behavior associated with water intake or loss. Consumptive behaviors may be affected by antecedent conditions of resource limitation, the direction of change in water availability, and limitation after alteration. Here we examine how increasing water availability in a dry floodplain environment alters consumption behavior. We thus predict two possible responses of trophic interactions to addition of free water, based on either increased activity rates, or decreases in consumption of moist food. Specifically, we predict that adding free water could lead to (1) stimulation of consumption and an increase in interaction strength between predators and prey by allowing quiescent water-stressed predators to more actively seek prey, in essence "wetting the appetite" for organic matter (i.e., increased water intake allows increased losses due to increased prey seeking), or (2) a decrease in consumption of moist food and interaction strength by quenching the predator's thirst for water-laden prey (like satiation, but for water). These predictions are based on a fundamental trade-off between management of water intake and losses and thus, this framework may provide a broad set of new hypotheses across current ecological theory. In summary, here, we combine physiological and behavioral perspectives with measurements of per capita interaction strength (IS), providing evidence that short-term terrestrial trophic interactions can be strongly and directly driven by water requirements instead of energy or nutrients.

MATERIALS AND METHODS

Study system

This experiment was conducted in the riparian floodplain forest adjoining Grayhawk Nature Center along the San Pedro River, in southeastern Arizona. From headwaters in Sonora, Mexico, the river flows north for over 160 km, across the U.S. border, connecting with the Gila River (Glennon 2002). The San Pedro River Valley lies along the transition zone between the Sonoran and Chihuahuan Deserts. Uplands are characterized by desert species such as Creosote Bush (*Larrea tridentata*) and cacti; the riparian zone is dominated by a gallery forest consisting of Fremont cottonwood (*Populus fremontii*) and Gooding willow (*Salix gooddingii*).

The San Pedro is dynamic in both space and time, with rapidly changing and highly fluctuating environmental conditions. Mean annual precipitation along the upper San Pedro is approximately 28 cm/yr and over 60% of this occurs during the monsoon months of July, August, and September (Stromberg et al. 1996). Monsoon floods can be extreme disturbance events, drastically altering the floodplain each year. After monsoon floods, the floodplain dries, with reduced flows throughout most of the year. Additionally, winter temperatures below freezing substantially reduce arthropod activity. During March–June, activity increases drastically as the area warms. However, little to no precipitation falls during this period. Air temperatures can reach $>40^{\circ}\text{C}$ and near surface soil moisture can be very low. Measurements in June of 2003 showed very low soil moisture throughout the floodplain ($5.6\% \pm 1.6\%$ by mass, J. Sabo, unpublished data). In addition to temporal changes, environmental conditions change rapidly with increasing distance to river. Near the river, saturated soil and surface flows raise humidity and provide abundant water to consumers (Sabo et al. 2008). Soil dries quickly with increasing distance to the river and humidity drops (Sabo et al. 2008; J. Sabo, unpublished data). Floodplains may be hundreds of meters wide; in these environments, less mobile consumers like crickets and spiders may obtain all their water from moist food (Sabo et al. 2008).

Ground-dwelling arthropods are highly tractable and represent an important component of the food web. Thus, our research focused on damp-loving field crickets (*G. alogus*, detritivores) and ground-dwelling wolf spiders (*H. antelucana*, dominant predators). These are two of the most abundant arthropod taxa along the San Pedro (Sabo et al. 2005). Further, *H. antelucana* is widespread across large portions of North America, including more mesic regions (Kaston 1978). Observations of *G. alogus* indicate that crickets are found under leaf litter during the day, sometimes aggregating, and adults occupy exposed areas at night. They often spread out considerably from a patch of litter into bare areas at sunset. During this period, they consume greenfall during the dry season (Sabo et al. 2008). During nighttime foraging and mating activities of *G. alogus*, wolf spiders (*H. antelucana* and others) have frequently been observed preying upon these crickets (though no quantitative estimates are available).

Field methods

During the dry season of 2007, eight pairs of $2 \times 2 \times 0.6$ m cages (0.2 m belowground, 0.4 m above) were distributed throughout a riparian floodplain forest along the San Pedro River, at Grayhawk Nature Center. Cages were wooden frames covered in standard fiberglass window screen and were open on the bottom to the soil (and thus any soil moisture), but closed on the top by lids. A strip of aluminum foil was glued inside along the sides of each cage to prevent escape of arthropods when lids were open. All cages were prepped by

attempting to remove all litter, vegetation, and arthropods greater than 3 mm in length. Approximately 0.1 m³ of loosely packed leaf litter was then added back to each cage, allowing for some clumping in one corner. Measurements taken by litter depth transects (a drastically different measurement method) in May of 2003 indicate that our addition is slightly low compared to average values at this site, but still within the range (mean = 0.21, range = 0–1 m³ litter per 4 m² ground surface; J. Sabo, *unpublished data*). Over the corner with litter clumping, we attached a construction paper shade-cover approximately 1 × 1 m. A wooden block measuring 61 × 15 × 5 cm was added to an unshaded portion of each cage.

All cages were stocked with 10 large juvenile or adult crickets (22.3 ± 0.24 mm head to tip of abdomen) collected greater than 100 m from the river, that were provided with water, ad libitum, overnight, in Ziploc bags. Each cage received 16 freshly picked cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*) leaves daily, arranged with four leaves of each type on each end of two wooden door shims (similar to Sabo et al. 2008). Each day, the previous day's leaves were removed and new leaves were added. According to Sabo et al. (2008), this level of leaf addition should have been sufficient to allow all 10 crickets to meet daily water demands (just cottonwood leaves equal between three and 10 times resting demand). One cage of each pair received two large (17.3 ± 0.85 mm head to tip of abdomen) *H. antehucana*. Cricket density reported by Sabo et al. (2008) was slightly lower than our density (2 vs. 2.5 crickets per m², respectively), but estimates used in that study were not intended to represent the maximum. Conservative estimates of mean spider density from visual transects outside of cages for a different experiment in June of 2007 were similar to our densities (0.45 vs. 0.5 per m², respectively, J. Sabo, *unpublished data*). Visual transects should result in low estimates, so actual mean densities are likely higher. Spider and cricket sizes were not recorded in either survey.

Four pairs of cages received ambient water levels (very dry), while four pairs received supplemental water. Water was added by use of R-Zilla Cricket Water Pillows (Central Garden and Pet Company, Walnut Creek, California, USA), small pillows of silicate gel that can hold up to 30 g of water each, retaining some water for more than 24 hours, even under hot and dry conditions. Crickets, spiders, and harvestmen were observed using pillows in other field experiments outside of cages; crickets and spiders have been observed using them in laboratory experiments; and crickets used pillows regularly in our field cages (K. McCluney, *personal observations*). These pillows provide water similarly to moist soil, allowing arthropods to suck water from the gel, or eat small amounts. Water-supplemented cages received five freshly hydrated water pillows each day, distributed along one side of each

cage, extending into the area of high leaf and shade cover.

On the eighth day after the experiment started, all crickets and spiders were caught, counted, and measured. Leaves were brought to the lab for image analysis. Crickets and spiders were returned to their cages, except in one case where accidental death of all crickets and spiders occurred for one pair of cages in the ambient treatment.

A large, atypical, day-long rain event occurred 11 days after initiation of the experiment, which caused little disturbance, but appears to have moistened the entire floodplain. After 14 days, we collected, counted, and measured all crickets and spiders from all cages. Spiders were brought back to the lab for identification. Leaves were brought to the lab. There were only four crickets remaining in some of the cages at this point. Continuing the experiment for much longer would have resulted in zeros, reducing our ability to distinguish per capita interaction strength (IS) between treatments.

It was found that two of the cages with water had two more crickets at the end of the experiment than at the middle. It is possible that we missed these crickets during the midpoint (day 8) sampling or that they entered the cages during a water or leaf replacement event in the intervening time period. However, changing the midpoint or final numbers of crickets to reflect these possibilities did not alter statistical conclusions.

Interaction strength.—Per capita interaction strength between crickets and spiders was calculated for each pair of cages for midpoint (day 8) and final (day 14) collections using the dynamic index (Laska and Wootton 1998, Berlow et al. 1999):

$$\alpha = \ln(C_s/C_{ns})/S \quad (1)$$

where α is the per capita interaction strength, C_s and C_{ns} are the number of crickets in cages with and without spiders, respectively, and S is the number of spiders. We chose to use this index as our response because (1) paired analysis reduces the influence of differences in environmental conditions between locations, (2) it gives a better measure of the strength of trophic interaction under changing prey density (i.e., it is harder to catch a single cricket than one of 10 crickets), and (3) it is a central concept of one of the major topics in community ecology, is related to both biodiversity and stability, and is commonly used by experimental and theoretical ecologists alike (Paine 1980, Laska and Wootton 1998, Berlow et al. 1999).

At midpoint sampling, two cages had only one spider found alive and at the end three cages had only one alive (midpoint: one dry, one wet; final: two dry, one wet). We do not know the causes for the disappearance of these spiders. At each collection, the number of live spiders was used in computations. Keeping the number of spiders at two during analyses did not alter statistical conclusions and only slightly reduced the magnitude of differences between treatments.

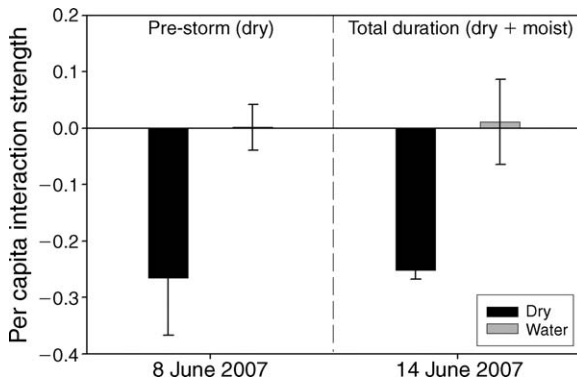


FIG. 1. Per capita interaction strength between cages with and without added water, before a large rainstorm, and for the duration of the experiment. The interaction during pre-storm, dry conditions, could not be separated from the interaction during post-storm, wet conditions. Differences are significant at the midpoint and across the whole experiment. Values are means, and error bars indicate \pm SE.

Residuals from the original data for interaction strength were slightly nonnormal (normal probability plots of residuals), but arcsine transformation improved normality (Lilliefors' test on residuals = 0.1413). Arcsine-transformed data were also equal in variance according to F tests (day 8, $F = 7.06$, $df = 3, 3$, $P = 0.143$; day 14, $F = 0.04$, $df = 2, 3$, $P = 0.073$). Therefore, we analyzed the data using rmANOVA.

Leaf consumption.—Leaf consumption was estimated by image analysis aided by SCIONImage (Scion Corporation, Frederick, Maryland, USA). Un-chewed wet and dry cottonwood and willow leaves were used to determine the relationship between leaf area and dry biomass using simple linear regression with zero as the constant and dry biomass consumption of each leaf was calculated as well as total consumption and per capita consumption. Differences in total per capita cottonwood leaf consumption between water treatments at the midpoint (day 8, before rain) and final (day 14, after rain) samplings were analyzed using a mixed-model ANOVA with random effects and included examination across time (SAS Institute 2005). However, in order to meet assumptions of normality (normal probability plots and Lilliefors test) and equal variance (residual vs. estimate plots), data were cube-root transformed before analysis (Lilliefors after transformation = 0.1165). Very little willow leaf material was consumed in any cages and thus results for willow leaves are not reported here.

RESULTS

After the first eight days of pre-storm, dry conditions, per capita interaction strength between wolf spiders and crickets was strong and negative ($\alpha = -0.266$) when predators were in ambient dry conditions, and was reduced to nearly zero ($\alpha = 0.001$) when given experimental water ad libitum (rmANOVA between

subjects $F = 11.9$, $df = 1, 5$, $P = 0.018$, Fig. 1). On a per capita daily basis, crickets consumed approximately 31 times more moist cottonwood leaf material without water than with experimental water (difference in ls means between water and dry on day 8, Tukey's $P < 0.0001$, Appendix A, Fig. 2). Consumption was near zero where water was added.

After rainfall, differences in per capita daily consumption of moist leaves by crickets were near zero for all treatments (no difference in ls means between water and dry on day 14, Tukey's $P = 0.1837$, Appendix A, Fig. 2). The difference in IS between water and no-water treatments did not change between midpoint (day 8) and endpoint (day 14) measurements despite rainfall on day 11 (time \times treatment $F = 0.15$, $df = 1, 5$, $P = 0.715$, Fig. 1).

DISCUSSION

Water availability strongly and directly altered the interaction between crickets and spiders and per capita consumption of green leaves by crickets. The IS for the ambient (dry) treatment recorded here (-0.266) was much stronger than the strongest reported values for three studies that also used the dynamic index of per capita interaction strength (-0.015 , -0.00009 , -0.027 ; Sala and Graham 2002, Taylor et al. 2002, Emmerson and Raffaelli 2004) over similar time periods (21, 14, and 2.5 days, respectively).

The artificial nature of field enclosures (cage effects) could have impinged on our results in a variety of ways, including alteration in microclimate, differences in home range, and an alteration of movement patterns and refugia options. However, our cages are fairly large (4 m^2). More importantly, our use of the dynamic index of per capita interaction strength and its paired design

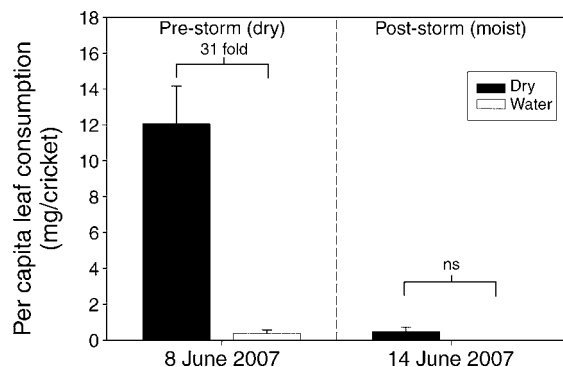


FIG. 2. Daily per capita consumption of moist cottonwood leaves by crickets in cages with and without added water, and before and after a large rainstorm. Brackets refer to the magnitude of the relative difference in cottonwood leaf consumption between means of treatments. Differences in leaf consumption are significant before the storm (31-fold difference in ls means between water and dry on day 8, Tukey's test, $P < 0.0001$), but not after the storm (no significant difference [ns] in ls means between water and dry on day 14, Tukey's test, $P = 0.1837$). Values are means and SE.

allows us to keep cage effects constant among treatments, isolating the influence of water availability from any (unknown) cage effects.

The mechanism linking water and cricket mortality is most likely a result of consumption by spiders. Though we did not directly observe predation events between spiders and crickets in our cages, our calculations of interaction strength compared paired cages with spiders to those without, but with the same water treatment, effectively controlling for non-spider-induced mortality. We note that between cages without spiders, in different treatments, there were no significant differences in cricket mortality and mortality was low in all no-spider cages. Estimates of mortality outside cages are unavailable; few studies have determined field mortality rates of crickets (but see Hein et al. 2003).

Our results suggest that adding free water produces a quenching effect, where both crickets and spiders decrease consumption of water-laden resources. In the short term, the spider-cricket IS was near zero when water was available. However, over slightly longer periods, IS would necessarily become negative for all treatments as spiders become limited by energy or nutrients and consume crickets. Further investigation is needed to determine if differences between water treatments would persist over longer periods. Our experiment provides direct evidence only for quenching when water is added. Addition of water to a dry environment was the only practical experimental design. However, one of our main questions in this system is how river drying influences riparian communities. Though we can make no solid conclusions about effects of water reduction on consumption behavior, we predict that compensation (increase in consumption with water reduction) would be a likely observation based on inference from the results found here. If compensation is common, removal of water (e.g., via stream drying) should drive spiders to consume more crickets in order to meet their daily water demand (Sabo et al. 2008). Direct support for the compensation hypothesis was found in lab trials (see Appendix B).

Consumption of picked leaves by crickets was directly and strongly altered by free water, with high consumption in dry cages before rainfall and very little consumption in any treatment after rainfall. Considering the large amount of dry litter in our cages, and our observations of crickets consuming it (K. McCluney, *personal observation*), it seems likely that crickets switch between consuming dry litter and moist plant material depending on free water availability. It is unclear if crickets switch between litter and still rooted plants outside cages.

Though our results strongly support a pattern of *quenching* of trophic effects by free water, the behavioral mechanisms of quenching are less clear. Spider-cricket quenching could arise from changes in either spider behavior (decreased search or attack rates) or cricket behavior (decreased movement, resulting in fewer

encounters with predators, or increased escape rates). These mechanisms are not mutually exclusive, and either way, water is driving the interaction. However, we discount cricket behavior as a mechanism for the observed differences in interaction strength in our experiment, because all cages had abundant moist food for crickets (3–10 times daily water demand; Sabo et al. 2008). Thus, spider search or attack behavior may have contributed to observed differences in consumption, but this topic deserves more attention.

Our results differ from those of several other studies examining the long-term, population effects of variation in water on trophic interactions (Preisser and Strong 2004, Spiller and Schoener 2008). These studies show stronger trophic effects with increasing water availability and suggest that higher trophic levels are more greatly impacted by environmental stress (water) than lower levels, similar to the hypothesis proposed by Menge and Sutherland (1987). Thus, they consider water in the context of theories of stress and disturbance developed in marine and rainforest ecosystems for non-resource stressors (Connell 1978, Menge and Sutherland 1987); but water can also serve as a vital resource that terrestrial consumers seek out via drinking or consumption of prey. Water stress can have multiple nonlethal effects on animals (for growth, see McCluney and Date 2008). Additionally, these studies of community effects of water have examined population-level phenomenon, where prolonged water stress may have increased mortality in a manner congruent with Menge and Sutherland's hypothesis, but sublethal effects of water-stress may have been missed.

Here, we examined the physiological link between water balance and consumer behavior and used IS as a response. This measure is the basis for one of three major schools of thought in food web ecology (Paine 1980, 1992), is often examined in the short-term (median = 22 days, Appendix C), and has recently received great attention (McCann et al. 1998, Ruesink 1998, Bascompte et al. 2005, Navarrete and Manzur 2008). However, more studies are needed that examine the connections between short-term measurements and long-term population dynamics.

Spiders and crickets in our study have particular tolerances for food and water limitation that may differ from other organisms (Hadley 1994). For instance, Gila monsters (*Heloderma suspectum*) spend much of the year underground and can store water in their bladders (Davis and DeNardo 2007). Increased water availability allows these animals to increase surface activity (Davis and Denardo 2006). This pattern may correspond more closely to our stimulation prediction, where increased water allows for greater consumption and is in agreement with studies showing stronger interactions with increased water. Disentangling the multiple factors that influence how variation in water affects trophic interactions and population dynamics in the short- and

long-term is an important direction for future research and discussion.

Dry lands occupy one-third of the earth's land area (Schlesinger et al. 1990). However, our results may also be relevant to moist regions that experience drought or surface water drying. We speculate that our study could provide important insights for these environments, since animals in these areas may not be well adapted to water stress. Further, temporary periods of drought often overlap reproductive periods and thus, may be more likely to have lasting consequences. Our observation that under dry conditions, water seems to be the ecological currency governing consumption behavior at multiple trophic levels indicates a role for water in understanding effects of global change on animal communities. Climate models predict significant positive and negative changes in precipitation and soil moisture, varying by region, but globally distributed. Many such changes have already been observed (Schlesinger et al. 1990, Intergovernmental Panel on Climate Change 2007). Additionally, water-body-drying events are occurring with increasing frequency, partly due to human consumption and river alteration (Gleick 2002, Stone and Jia 2006, McKinnon 2007). An energy or nutrient based paradigm alone is not likely to fully predict the effects of these globally distributed changes on terrestrial animal communities. Our results suggest geographic alterations in aridity predicted by recent climate models will lead to dramatic shifts in consumption behavior, and the direction and magnitude of these effects may be best understood by including water as the salient ecological currency.

ACKNOWLEDGMENTS

We thank P. Umaretiya for Appendix B; C. Soykan, E. Hagen, J. Kirchner, L. Thompson, D. Smith, N. McCluney, and Y. Marusenko for field assistance; S. Anderson and Grayhawk Nature Center; J. Porter for cage construction; A. Rosenthal for statistics; J. Slowik and A. Spriggs for spider identifications; and D. Spiller, J. Elser, J. Davis, and the Sabo lab for reviews. Funding was provided by EPA STAR grant FP-91649201 to K. McCluney and the Brian Daniel Corrigan Foundation. Aquaria for lab experiments were provided by the Uhlmann Fund. K. McCluney designed and conducted experiments, analyzed results, and wrote the manuscript. J. Sabo contributed to the design of the field experiment, data analysis, and writing of the manuscript.

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APPENDIX A

Photographs of field experiment and ANOVA table of leaf consumption by crickets in field experiment (*Ecological Archives* E090-098-A1).

APPENDIX B

Methods and results of lab experiments examining consumption of crickets by spiders with varying water (*Ecological Archives* E090-098-A2).

APPENDIX C

Tabular results of a review of other experimental examinations of per capita interaction strength (*Ecological Archives* E090-098-A3).