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Animal water balance drives top-down effects in a riparian forestimplications for terrestrial trophic cascades

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RUNNING HEAD: Water balance mediates top-down effects

TITLE: Animal water balance drives top-down effects in a riparian forest—implications

- **for terrestrial trophic cascades**
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Abstract

 Despite the clear importance of water balance to the evolution of terrestrial life, much remains unknown about the effects of animal water balance on food webs. Based on recent research suggesting animal water imbalance can increase trophic interaction strengths in cages, we hypothesized that water availability could drive top-down effects in open environments, influencing the occurrence of trophic cascades. We manipulated large spider abundance and 14 water availability in 20×20 m open-air plots in a streamside forest in Arizona, USA, and measured changes in cricket and small spider abundance and leaf damage. As expected, large spiders reduced both cricket abundance and herbivory under ambient, dry conditions, but not where free water was added. When water was added (free or within moist leaves), cricket abundance was unaffected by large spiders, but spiders still altered herbivory, suggesting behavioural effects. Moreover, we found threshold-type increases in herbivory at moderately low soil moisture (between 5.5% and 7% by volume), suggesting the possibility that water balance may commonly influence top-down effects. Overall, our results point towards animal water

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balance as an important driver of direct and indirect species interactions and food web dynamics

in terrestrial ecosystems.

KEY WORDS: Water web, food web, drought, precipitation, predation, herbivory

Introduction

 The evolution of terrestrial life has been driven by the challenge of maintaining water balance with scarce freshwater resources, but effects of animal water limitation on terrestrial food webs have received little attention, in contrast to plant-mediated bottom-up effects [e.g. [1,](#page-15-0) [2-5\]](#page-15-1). This is a significant gap in our understanding of ecological dynamics, since over 40% of the earth's land surface is classified as drylands [\[6\]](#page-16-0) and precipitation limits diversity of plants and animals at all but the highest latitudes globally, even outside of drylands [\[7\]](#page-16-1). Moreover, both animal water demand and the availability of water are being altered by global changes in temperature, precipitation, urbanization, and water infrastructure [\[8\]](#page-16-2). If water balance influences food webs, it may also alter ecosystem form and function in ways that directly impact humans (e.g. crop production in agroecosystems).

 Water availability likely has both bottom-up and top-down effects on food webs [\[9\]](#page-16-3), but evidence for top-down effects comes mostly from observational research [\[5,](#page-16-4) [10-12\]](#page-16-5), limited field manipulations [\[13,](#page-17-0) [14\]](#page-17-1), or cage experiments [\[15\]](#page-17-2). This evidence suggests that consumers may meet water demands by consuming large amounts of moist food when environmental water sources (e.g. saturated soil or open water) are unavailable [\[9,](#page-16-3) [10,](#page-16-5) [15\]](#page-17-2). In these situations, terrestrial food webs can be viewed as water webs, with water driving trophic interactions [\[15\]](#page-17-2).

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 Large scale, open-air manipulative experiments examining the direct importance of animal water balance in structuring food webs are generally lacking [\[but see 16\]](#page-17-3).

 Systems with strong top-down effects can shift dramatically with relatively small changes to the food web, leading to trophic cascades [\[17-19\]](#page-17-4). Trophic cascades, where predators affect the abundance of primary producers by altering density or behaviour of intermediate trophic levels [sensu [20,](#page-18-0) [21,](#page-18-1) [22\]](#page-18-2), were once considered to be "all-wet," occurring predominantly in freshwater ecosystems [\[23-25\]](#page-18-3). However, recent research has demonstrated that terrestrial trophic cascades are common and widespread, but often difficult to detect [\[17,](#page-17-4) [26,](#page-18-4) [27\]](#page-18-5). Trophic cascades may be driven by direct reductions in density of herbivores by predators, or by predator modifications of herbivore foraging behaviour (e.g. "fear") [e.g. [28,](#page-18-6) [29-31\]](#page-19-0). Previous research suggests that the magnitude of top-down effects may be influenced by consumer size and metabolic rate, the existence of plant defences, the diversity of herbivores, the choice of plant response metric, and environmental conditions like solar radiation, temperature, rainfall, or disturbance [\[5,](#page-16-4) [26,](#page-18-4) [27,](#page-18-5) [32,](#page-19-1) [33\]](#page-19-2). Additionally, trait-mediated indirect interactions, like anti- predator behaviour, often play a large role in driving these cascades [\[28,](#page-18-6) [29,](#page-19-0) [31,](#page-19-3) [34\]](#page-19-4), with the strength of these effects, relative to density-mediated indirect interactions (direct consumption), likely driven by predator hunting modality (i.e. sit and wait) and habitat use relative to prey [\[29\]](#page-19-0). As yet, the importance of animal water balance in determining the strength of top-down effects or the likelihood of trophic cascades, has received surprisingly little attention. Previous work has shown that water balance can influence consumption of moist food for particular consumers [\[9,](#page-16-3) [15\]](#page-17-2). We hypothesized that this alteration of consumption would lead to changes in the strength of top-down effects in real food webs. We designed and executed a large and

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Overview

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 rains began during the last few days of experimental surveys, in the third experimental period (25 June, Figure 2), and major flood disturbance occurred shortly thereafter, which would have prevented continuation of the experiment. Flooding during the monsoon season is likely to be important in driving population dynamics for our focal species, but in this study, we focused on the dry season to help us better understand how animal water balance influences food web dynamics in general.

Design

 After the initial pre-manipulative measurement period, we began reducing the abundance of the top invertebrate predators, large wolf spiders (mostly *Hogna antelucana,* >1 cm head to cephalothorax), via nightly removal by hand capture (Electronic Supplementary Materials, Text S1). Removal occurred across plots (4 treatment plots plus 3 additional spider removal only plots, Electronic Supplementary Materials, Figure S1) within three randomly selected sections of the two experimental floodplains, leaving another three sections with ambient large spider abundance. Floodplain sections were separated from one another by >60 m of floodplain forest (Electronic Supplementary Materials, Figure S1). We manipulated large spider abundance but not cricket abundance because we were primarily interested in the influence of water balance on top-down effects from spiders to crickets to leaf consumption. Additionally, simultaneously manipulating spider and cricket abundance would be untenable in large, open-air plots. Using a split-plot design, we crossed the spider manipulations with alteration of water availability, either directly as free water (R-Zilla Cricket Water Pillows—pouches filled with a hydrated polymer that moistens a cotton mesh surface; Central Garden and Pet Company, Walnut Creek, California, USA) or indirectly as "trophic water" contained within freshly picked

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 near the centre of each floodplain section using a Delta-T soil moisture sensor (ML2X Theta Probe with HH2 meter, Dynamax, Inc.). We also measured ground temperature using Hobo micro-station data loggers equipped with smart sensors (Onset, Bourne, Massachusetts, USA) housed in 15 x 21 x 19 cm white, plastic, ventilated, radiation shields, placed on the ground. *Data Processing and Statistical Analysis* Analyses of nightly surveys were conducted using likelihood ratio tests of linear mixed models, with time, water addition, and spider removal as fixed factors, and floodplain section, plot, and transect as nested random factors. Fixed factors were dropped, one at a time, from a full model, testing for significant changes in likelihood [\[sensu 40\]](#page-20-2). If a significant interaction between water addition and spider removal was detected, we tested our specific predictions using post-hoc general linear hypothesis tests (Dunnet's), examining if large spiders had an effect on

crickets, small spiders, or leaves under different water addition treatments. All analyses were

conducted in R v. 3.0.2 [\[41\]](#page-20-3), with nlme [\[42\]](#page-20-4), lme4 [\[43\]](#page-20-5), and multcomp [\[44\]](#page-20-6) packages. We also

examined the relationship between rates of herbivory and soil moisture in the true control plots

(Electronic Supplementary Materials, Text S1, Figure S1) across the entire experiment using

glmm on individual leaves and breakpoint regression [\[via the 'segmented' package in R, 45\]](#page-20-7) on

168 plot averages. See Electronic Supplementary Materials Text S1 for more details.

Results

Environmental Conditions

 Two large rain events with an intervening dry, hot period characterized our 51-day study (Figure 2A). Declining soil moisture and streamflow followed the initial, aseasonal rain event, with complete river drying prior to initiation of experimental manipulations (day 13). Another

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rain event near the end of the experiment (during the simulated drying period) raised soil

- moisture and signalled the start of the monsoon season.
- *Efficacy of spider removal*
- We removed 2,691 large ground spiders (mostly *Hogna antelucana*) over 35 days (May
- $23rd$ June 15th), significantly lowering the abundance of this top invertebrate predator (Figure
- 2B-D; Electronic Supplementary Materials, Table S1). Large spider abundance declined across
- all plots—possibly reflecting natural seasonal variability unrelated to removal—but the rate of
- decline was 14X greater in removal plots than the ambient plots (Figure 2C); this translated into
- a mean of a 55% reduction in large spiders in the reduced spider plots during the
- 183 supplementation period (0.044 vs 0.020 spiders per $m²$). We found no significant effects of water
- manipulation on large spider abundance (Table S1).
- *Predator effects on primary consumers—crickets—with altered water resources*
- 186 Large spiders reduced the abundance of crickets (*Gryllus alogus*) under dry ambient
- conditions, but not when either free water or moist leaves were experimentally added (i.e.,
- significant water × spider interaction, Tables 1, S1; Figure 3). Cricket abundance increased in all
- plots across the first two experimental periods, but spiders reduced the rate of increase by 37% in
- dry ambient conditions (Figure 3); this translated into a mean of a 23% reduction in crickets in
- ambient spider, dry control plots, during the supplementation period (1.48 vs 1.14 crickets per
- $m²$). With cessation of water addition (simulated drying) in the third experimental period, cricket
- abundance declined, especially in moist leaf addition plots, but this reduction did not appear to
- be influenced by large spiders according to post-hoc tests (Figure S2; Table S2).
- *Predator effects on intra-guild predators—small spiders—with altered water resources*

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 soil moisture declined naturally (see Figure 2), but, the magnitude differed between water and spider removal treatments (Figure 3; Tables S1, 1). Spiders depressed herbivory under dry ambient conditions and where moist leaves were added, but slightly enhanced leaf consumption with free water addition (Figure 3; Table 1). These effects were reversed on the final date of the experiment, when soil moisture was again high due to rainfall, with leaf consumption near zero in all plots (Figure S2; Table S1&2).

Soil moisture and herbivory

 Across treatments, herbivory was most strongly and significantly correlated with soil moisture (Table S1), with herbivory dropping sharply above 6.8% soil moisture (the maximum

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 value with > 50% consumption of leaves) or with consumption declining at 5.51% soil moisture on average (breakpoint regression; Figure 4).

Discussion

 Here we show that variation in water availability can modify the strength of top-down effects (Figure 1B). Population-level effects of large spiders on crickets varied with water availability, as predicted from previously observed shifts in per capita consumption in cages [\[15\]](#page-17-2). Specifically, large spiders reduced cricket populations under dry ambient conditions, but had no effect with water supplementation (Figure 1, B1 vs B2). This result followed expectations from previous research in cages [\[15\]](#page-17-2), and thus supports the hypothesis that short-term, small- scale changes in per capita effects can roughly predict longer-term population-level dynamics [\[19\]](#page-17-5). Similarly, as predicted, large spiders had positive effects on moist leaf material (reduced herbivory) under dry conditions (Figure 1, B1), but in contrast to predictions (no effect), large spiders increased herbivory where direct free water was added (reverse of a trophic cascade; Figure 1, B2). Moreover, large spiders reduced herbivory with moist leaf addition, even though the abundance of crickets was unaffected by large spiders (Figure 1, B3). Water also influenced the effects of large spiders on small spiders, but the mechanism remains unclear, requiring further exploration. Taken together, our results suggest that free water availability controlled the size and direction of multi-level top-down effects in this system, but not always as predicted. The increase in herbivory associated with spiders when free water was added (reverse trophic cascade) was unexpected (expectation = no effect). Although we cannot directly test the mechanism behind this observation, we hypothesize it may be due to large spiders deterring crickets from accessing water pillows [\[video observation, J. Sblendorio and L. Ford II; sensu 46\]](#page-20-8),

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 forcing crickets to rely more greatly on moist leaves to meet water demands [\[10\]](#page-16-5). Another unexpected result was the lack of an effect of spiders on cricket abundance in moist leaf additions. We hypothesize this could be due to high rates of recruitment of crickets to these plots masking potential evidence of top-down effects (see rate of increase in crickets in moist leaf plots in Figure 3) or perhaps could be associated with an increased water content of crickets in those plots leading to lower per capita consumption by spiders. Despite the lack of an effect of large spiders on cricket abundance with moist leaf additions, large spiders still reduced herbivory in that treatment (see spider effect on moist leaves in Figure 3 & Figure 1, B3). Although we cannot directly test a mechanism for this observation, we hypothesize that this could be a consequence of a trait-mediated indirect interaction—"fear" of predation by large spiders could have led to reductions in rates of leaf consumption, especially when these leaves were more abundant [sensu [29,](#page-19-0) [46\]](#page-20-8). However, we admit there are other, more complex possibilities. For instance, if spider consumption of crickets led to compensatory dispersal of crickets into high spider plots at higher rates, new crickets could have changed competitive interactions within these plots or showed other differences in behaviour that could have reduced herbivory. But, overall, we believe it is most likely that trophic cascades in this system are being driven by a combination of density-mediated indirect interactions (consumption) and trait-mediated indirect interactions (behaviour), agreeing with expectations from theory for a sit-and-pursue predator with prey confined to the same habitat as predators [\[see](#page-19-0) [29\]](#page-19-0). Moreover, although other possibilities exist, we hypothesize that the balance of trait- mediated and density-mediated effects may depend on water availability—consumers may perform a cost-benefit analysis: with limited water (free or in food), direct consumptive effects

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 may outweigh behavioural effects, whereas with greater water availability (free or in food) behavioural effects may become more pronounced. We believe that water balance may play a large role in driving the behaviour of terrestrial animals—dehydration can occur quickly and may pose more certain risks than predation (perhaps epitomized by species interactions surrounding watering holes in the African savanna [\[47\]](#page-21-0)). But testing the hypotheses outlined above requires additional experimentation.

 Levels of leaf damage were highly correlated with soil moisture (more strongly than water addition treatments) with a non-linear, threshold-type transition from almost full consumption to almost zero consumption between 5.5% (breakpoint regression) and 6.8% volumetric soil moisture (maximum soil moisture with > 50% leaf consumption). This level likely represents the point at which crickets switch from obtaining water from moist leaf material to obtaining water from environmental sources. We believe this transition point could vary considerably among taxa and ecosystems, due to differences in physiological traits (e.g. cutaneous water loss), drivers of water loss (e.g. temperature, humidity), and availability and quality of trophic water sources (e.g. chemically defended leaves). However, to provide some guidance as to the potential frequency of water-mediated top-down effects, we examined volumetric soil moisture measurements across the US using the COSMOS Soil Moisture Network database [\[48\]](#page-21-1) and found that soil moistures below 6.81% can be found in 49% of the 65 US measurement locations, over the seven year period from 2008-2014—even mesic locations in the southeastern US and in northern Wisconsin and Michigan showed values below this threshold, but the greatest frequency was within the US sunbelt (Electronic Supplementary Materials, Figure S5). These results correspond well to previous suggestions that patterns of

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DATA ACCESSABILITY: Data is available in the Electronic Supplementary Material.

COMPETING INTERESTS: We have no competing interests.

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AUTHOR CONTRIBUTIONS: KM designed, conducted, and analyzed the study and wrote

- the manuscript. JS provided advice on the design and analysis of the study and edited the
- manuscript.

ACKNOWLEDGEMENTS

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Citation: 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: Biological Sciences **283**(1836). <http://rspb.royalsocietypublishing.org/content/royprsb/283/1836/20160881.full.pdf>

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Figure and Table Captions

 Figure 1. Comparison of predicted and observed effects of large (>1 cm) ground spiders, under three water treatments, on a desert riparian food web. The water drop symbol indicates the experimental supplementation of free water (via water pillows) and the leaf symbol indicates fluxes of water in moist leaf material (natural and experimental). Water was supplemented 2.5X the ambient rate of water flux (via natural greenfall). The width of arrows represents the qualitative size of fluxes of water (grey arrows) or the strength of top-down effects (black arrows). Mathematical symbols indicate direction of effects, while numbers are parameter estimates of the rate of change (see Table 1). Under dry ambient conditions (left) and with added moist leaves (right), we expected large spiders to have strong negative effects on cricket abundance and positive effects on leaf abundance, but we expected these effects to disappear with free water (middle). Additionally, we expected large spiders to switch between consumption of crickets (without water) and small spiders (with water). Observed patterns matched the expectation that free water would greatly influence top-down effects. But water addition was insufficient to "quench" cricket leaf consumption (*sensu* McCluney and Sabo 2009), large spiders did not reduce cricket abundance with moist leaf additions, and the effects of large

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spiders on herbivory where water was added were likely behavioural, since there were no effects

of large spiders on cricket abundance in those treatments. Effects of large spiders on small

spiders also did not match expectations, with large spiders positively affecting small spiders

under dry ambient conditions, but having no effects in other treatments.

 Figure 2. Changes in soil moisture (A), air temperature (A), and spider abundance (B-D) over the duration of the experiment. Error bars are standard error of the mean. C and D represent estimates of the rate of change in large spider abundance per unit time, between each of the experimental periods, from model parameter estimates, which controls for plot differences. Spider removal significantly reduced the abundance of large spiders by the end of the supplementation period (Table S1).

 Figure 3. Effects of large spiders on crickets, small spiders, and leaves, reported as the rate of change from the initial, pre-manipulation period to the end of the spider removal, water addition period. Plots are divided into ambient water plots ("Control," "C," black symbols), free water supplemented plots ("Water," "W," blue symbols), and moist leaf supplemented plots ("Moist Leaves," "ML," green symbols). "A" and "R" on the X-axes refer to ambient and reduced densities of large spiders. Error bars are standard error of the mean. Effect sizes are estimates of the rate of change in each response per unit time (3-day survey blocks for crickets and spiders, experimental periods for leaves), based on model parameter estimates, which controls for plot differences. Large spiders had a significant negative effect on crickets in control plots and positive effect on moist leaves in all treatments (but note the effect is opposite for free water)

Table 1

Media summary

Despite the clear importance of water balance to the evolution of terrestrial life, much is unknown about the effects of animal water balance on food webs. Here we show that the amount of water available to predators (spiders) can change the effects of these predators on prey (crickets) and vegetation (moist leaves). Moreover, water balance appears to drive the consumption of moist food under soil moisture conditions that are currently common across the US and may become increasingly common with climate change. Thus, rainfall and drought may influence how predators control prey and rates of herbivory.

Electronic Supplementary Material

Text S1. Detailed Methods

Study Site and Species Descriptions

The experiment was conducted in a pair of large adjoining floodplain forests along the San Pedro River, in southeastern AZ, USA. Each floodplain was 3-4 ha in size and was dominated by an overstory of Fremont cottonwood (*Populus fremontii*) and Goodings willow (*Salix goodingii*), with an understory of tamarisk (*Tamarix* spp.), seepwillow (*Bacharis* spp.), and mesquite (*Prosopis velutina*). In riparian forests along the San Pedro, moist green cottonwood leaves fall to the forest floor ("greenfall") daily, providing a flux of groundwater to aboveground consumers (Sabo et al. 2008). Dry leaf litter, mostly from cottonwoods, dominated the ground cover, but bunch grasses, primarily Johnson (*Sorghum halepense*) and Sacaton (*Sporobolus wrightii*) were present in abundance at some locations. In general these grasses were dormant and dry during the study. Uplands, not directly involved in this study, were characterized by plants of the Chihuahuan desert, including creosote (*Larrea tridentata*) and yucca (*Yucca* spp.). Previous work has demonstrated that riparian habitat along the San Pedro is, in general, cooler and more humid than desert uplands in this semi-arid region (Sabo et al. 2008).

Damp-loving field crickets (*Gryllus alogus*) were the numerically dominant low-level omnivorous consumer in these riparian forests, while the wolf spider *Hogna antelucana* was the largest, most abundant invertebrate predator. *G. alogus* is endemic to the southwestern US, but *H. antelucana* has a widespread distribution across the US (Shorthouse 2009). In several previous studies as well as this one, *G. alogus* has been observed consuming dry leaf litter, seeds, moist green leaves, and dead or immobilized conspecifics, while *H. antelucana* has most commonly been observed preying on *G. alogus*, but is a generalist sit-and-pursue predator (K. McCluney, *pers obs*). Other, less numerous, but fairly common invertebrates in this food web include roaches (Order Blattodea), camel crickets (Family Rhaphidophoridae), ground beetles (Tenebrionidae: *Eleodes*), and a variety of smaller spider species (e.g., *Pardosa* spp.). Additionally, tree and ground lizards, medium sized mammalian carnivores or omnivores, and insectivorous birds likely prey on ground-dwelling arthropods in this system (Soykan and Sabo 2009, K. McCluney, pers. obs.).

The San Pedro River is one of the last free-flowing (undammed) rivers in the American west and has a high diversity of birds (100 breeding species, 250 migratory), mammals (80 species), and reptiles (65 species) (Stromberg and Tellmann 2009). Along the 140 km of this south to north flowing dryland river, sections can be found that flow perennially, intermittently, or ephemerally (Turner and Richter 2011). The hydrology and ecology of the San Pedro are driven by distinct seasonality, with a hot, dry early summer (May-June) and a wet monsoon (July-September) season. Most of the yearly precipitation falls in the monsoon season, resulting in large floods that can create major disturbance events in the river and the floodplain.

Design

Previous pilot work suggested that dispersal of spiders over short distances was significant (observations of marked individuals traveling >30 m in less than a week). Therefore, complete randomization of spider and water treatments would have produced unintentional adjacent removal or spillover of spiders, diluting the effect of the removal treatment—a central goal of the experiment. To maximize treatment success, we set up our plots with restricted randomization in a classic split-plot design (Figure 2), in which spider removal plots were randomly assigned to three blocks within six regions of the floodplain, separated by >60 m from ambient spider block. Water treatments (free and trophic) and controls were randomly assigned to plots within each of these regions.

Large spider removal was conducted nightly, directly following completion of surveys in each plot. Large spiders (>1 cm head to cephalothorax) were removed from each spider removal plot by two individuals searching for 6 mins (8 mins on the first night) with the same headlamps as those used for surveys. Spiders were also removed from 3 "ghost" plots in each spider removal section, immediately adjacent to experimental plots, but no further activities were conducted in these plots (Figure S1). These plots were used solely to increase our removal rate of spiders in the reduction regions of the floodplain.

Water treatments were applied to a column of 3 plots that bordered each other on a side (Figure S1), with either free water or trophic water added to the plots on each end (randomly assigned), with the middle plot left as a control ("middle control"). Additionally, we created another control plot, spaced at least 20 m from the other plots ("true control"). Middle control plots were excluded from analyses and discussion within this manuscript, since their purpose was to examine arthropod movement rather than understand how water influenced trophic cascades.

During the supplementation period, water pillows or freshly picked cottonwood leaves were added daily as resource "patches." Each "patch" was added to each plot in a random location by creating a "pace-sized" grid for each plot and using a random number generator, with replacement, to determine the location of each resource patch in terms of number of paces in each direction. Thus resource patches were randomly distributed in each plot with some locations having up to two (maximum observed in our random draws) resource patches clumped together, but with most locations having only one resource patch or none. This design also ensured that the number of resources on or off a transect varied randomly. Each plot received 25 resource patches.

Water pillows contain approximately 30 mL of water and can stay wet for extended periods of time. Each plot received 750 mL of additional water per day, a rate equivalent to 2.5x the rate of water flux naturally occurring in greenfall (Sabo et al. 2008). Water pillows are made commercially for the pet industry, specifically for house crickets and hermit crabs, but we have successfully used this product in the lab and field for a variety of arthropods (McCluney and Sabo 2009). In all, we added 150 water pillows per day across all plots (4.5 L of water), or 3,450 (103.5 L of water) over the course of the experiment.

Moist green leaves were picked from the same location each day, from trees at a similarly sized floodplain upstream of the study site. To equal an equivalent volume of water as provided in the water pillows, each moist leaf patch consisted of 19 cottonwood leaves placed in a mesh bag with 2.5 cm openings. This equaled 475 leaves per plot, per day, 2,850 leaves across all plots each day, and 65,550 across the addition period. In both cases, water was supplemented at 2.5 times the ambient rate of cottonwood greenfall water flux (Sabo et al. 2008). However, crickets

may compete for access to water pillows and defend them against conspecifics (unpublished data). Thus, the relative delivery of water to crickets may have differed between these treatments, since there was substantially greater surface area of bags of moist leaves than of water pillows and we commonly observed >10 crickets on a single bag of leaves, but rarely this many on a water pillow, and usually less than 5 at a time (unpublished data).

Surveys

To reduce the perception of observer effects as treatment effects, the same pair of observers would conduct surveys for 10 days at a time, with transitions to a new pair of observers timed to avoid experimental transition periods. The location of initiation of surveys rotated nightly and responses were averaged across a complete rotation of starting locations (3 days) to reduce effects of temporal differences in activity.

Data Processing and Statistical Analysis

In statistical analyses, responses were typically expressed as the natural log of 3-day means of the count data, to reduce effects of a different starting location on each of those nights and to meet model assumptions (normality). We tested if temporal autocorrelation was important by comparing models that assumed compound symmetry or autoregressive variance-covariance structures and picked the best model, based on AIC, for subsequent analysis. Analyses of leaf damage were conducted similarly, but due to the non-normal, proportion-based measurements, we compared generalized linear mixed effects models with a binomial link function.

To properly compare experimental periods, we divided the analyses, first comparing changes between the initial pre-treatment period and the supplementation and spider removal period. Then we separately examined the post-supplementation (but still spider removal) simulated drought period.

Comparison of Soil Moisture-Herbivory Relationships With US Soil Moisture Patterns

We compared the relationship between soil moisture and herbivory found in our study with measurements from the COSMOS soil moisture sensor network (Zreda et al.) from 2008- 2014 to predict the potential frequency of animal water stress across the US. Specifically, we divided the number of observations of soil moisture below the threshold value for water limitation (from experimental measurements) by the total number of observations, for each site. We excluded measurements below 35 cm soil depth and from November through March each year, focusing on ground arthropod available soil moisture during the growing season. We also excluded a limited number of values lower than 0% or higher than 100% to remove erroneous measurements.

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Figure S1. A) Site map with water treatments denoted by colors and spider treatments denoted by the presence of a line through the plot. Ambient plots between water addition plots ("middle control") were excluded from analysis and discussion in this paper, with comparisons only made with adjacent ambient plots separated by >20 m ("true control"). Additional spiders were removed from "ghost" plots, but responses were not measured. See methods and Appendix B for more thorough description. B) Field crickets (*Gryllus alogus*) drinking water from the surface of a water pillow. C) The wolf spider *Hogna antelucana* hunting the field cricket *Gryllus alogus* on added leaves (by JL Sabo).

Figure S2. Changes in cricket abundance associated with large spider removal for each water treatment. Plots are divided into ambient water plots ("Control," white background, top row), free water supplemented plots ("Water," blue background, middle row), and moist leaf supplemented plots ("Moist Leaves," green background, bottom row). A and R on the X-axes refer to ambient and reduced densities of large spiders. Error bars are standard error of the mean. D-I represent estimates of the rate of change in cricket abundance per unit time, between each of the experimental periods, based on model parameter estimates, which controls for plot differences. Spider removal significantly increased the abundance of crickets in ambient dry conditions only (Table 1).

Figure S3. Changes in small spider abundance associated with large spider removal for each water treatment (A-C). Plots are divided into ambient water plots ("Control," white background, top row), free water supplemented plots ("Water," blue background, middle row), and moist leaf supplemented plots ("Moist Leaves," green background, bottom row). A and R on the X-axes refer to ambient and reduced densities of large spiders. Error bars are standard error of the mean. D-I represent estimates of the rate of change in small spider abundance per unit time, between each of the experimental periods, based on model parameter estimates.

Figure S4. Changes in leaf consumption associated with large spider removal for each water treatment (A-C). Plots are divided into ambient water plots ("Control," white background, top row), free water supplemented plots ("Water," blue background, middle row), and moist leaf supplemented plots ("Moist Leaves," green background, bottom row). A and R on the X-axes refer to ambient and reduced densities of large spiders. Error bars are standard error of the mean. D-I represent estimates of the rate of change of leaf material per unit time, between each of the experimental periods, based on model parameter estimates, which controls for plot differences. Spider removal led to small decreases in leaf material in dry control (D) and moist leaf addition (H) treatments, but slight increases in water addition plots (F) (change from experimental period 0 to 1, Table 2). Changes from experimental period 1 to 2 (E, G, I) are just reversals of previous patterns as water limitation was alleviated by rainfall (see Figure 2A).

Figure S5. Expected distribution and frequency of water-limited trophic interactions during the growing season (April-October), based on extrapolation from experimental measurements to observations in the COSMOS soil moisture network. Coloration represents the frequency of observations shallower than 35 cm that fall below the maximum cutoff for water-limited herbivory observed in experimental work (6.8% volumetric soil moisture). 49% of all stations in the US and 63% of all stations in the sunbelt (below dashed line) have experienced soil moistures that could promote water limited trophic interactions.

Figure S6. Expected average distribution and frequency of water-limited trophic interactions during the growing season (April-October), based on extrapolation from experimental measurements to observations in the COSMOS soil moisture network. Coloration represents the frequency of observations shallower than 35 cm that fall below the breakpoint regression suggested average cutoff for waterlimited herbivory observed in experimental work (5.51%). 40% of all stations in the US and 56% of all stations in the sunbelt (below dashed line) have experienced soil moistures that should promote water limited trophic interactions.

Table S1. Effects of treatments (or soil moisture) on measured response variables, shown as the effect of removing each term from the full model (likelihood ratio tests).

Table S2. Post-hoc multiple comparisons, examining the effect of spiders, under different water addition treatments.

*Not log transformed, just the change per unit time

Site	Latitude	Longitude	freq.6.8	freq.5.51	nobs
Austin Cary	29.738	-82.219	0.048	0.006	6989
Freeman Ranch	29.949	-97.997	0.000	0.000	12447
JERC	31.236	-84.462	0.231	0.026	8572
San Pedro 2	31.562	-110.140	0.336	0.138	12295
Kendall	31.737	-109.942	0.512	0.326	15536
Rancho No Tengo	31.744	-110.022	0.775	0.655	3817
Lucky Hills	31.744	-110.052	0.582	0.404	5134
Santa Rita Mesquite	31.820	-110.840	0.598	0.427	3141
Santa Rita Creosote	31.909	-110.839	0.256	0.000	5455
Mount Lemmon	32.442	-110.782	0.000	0.000	3521
Biosphere 2	32.580	-110.851	0.936	0.717	11857
Jornada Mixed Shrubland	32.580	-106.600	0.430	0.285	3098
Savannah River	33.383	-81.566	0.306	0.002	3010
Desert Chaparral UCI	33.609	-116.451	0.580	0.311	8446
Coastal Sage UCI	33.734	-117.696	0.010	0.000	17805
Goodwin Creek	34.255	-89.874	0.002	0.001	10648
Sevilleta New Grass	34.400	-106.674	0.918	0.359	184
Hauser Farm South	34.577	-111.859	0.000	0.000	3487
Hauser Farm North	34.580	-111.863	0.000	0.000	3510
Coweeta	35.066	-83.437	0.000	0.000	6616
Bushland	35.188	-102.096	0.000	0.000	11977
Flag Ponderosa Pine	35.439	-111.804	0.000	0.000	12490
Flag Wildfire	35.446	-111.772	0.000	0.000	12499
Santa Fe Watershed-SF1	35.679	-105.827	0.000	0.000	4941
Jonesboro	35.760	-90.762	0.000	0.000	2416
VCNP CZO	35.890	-106.533	0.004	0.000	13914
Chestnut Ridge NOAA	35.931	-84.332	0.003	0.001	11688
SMAP-OK	36.064	-97.217	0.074	0.013	20276
ARM-1	36.605	-97.488	0.009	0.000	20251
Soaproot	37.031	-119.256	0.000	0.000	16055
P301	37.068	-119.194	0.487	0.264	16091
UVA	37.923	-78.274	0.000	0.000	7997
Tower Ruin	38.117	-109.718	0.377	0.284	7905
Lower Salt Creek	38.129	-109.735	0.490	0.424	7971
Tonzi Ranch	38.432	-120.966	0.000	0.000	16173
Mozark	38.744	-92.200	0.000	0.000	12956
Sterling	38.974	-77.485	0.000	0.000	6928
Beltsville	39.030	-76.846	0.000	0.000	12080
Manitou Forest Ground	39.101	-105.103	0.171	0.027	14530

Table S3. The frequency with which soil moistures from the COSMOS soil moisture network fell below the maximum (6.8%) or breakpoint regression suggested average (5.51%) cutoff for water-limited herbivory from experiments.

