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GREENFALL LINKS GROUNDWATER TO ABOVEGROUND FOOD WEBS IN DESERT RIVER FLOODPLAINS

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Abstract. Groundwater makes up nearly 99% of unfrozen freshwater worldwide and sustains riparian trees rooted in shallow aquifers, especially in arid and semiarid climates. The goal of this paper is to root animals in the regional water cycle by quantifying the significance of groundwater to riparian animals. We focused our efforts on the cricket, *Gryllus alogus*: a common primary consumer found in floodplain forests along the San Pedro River, in southeast Arizona, USA. Cottonwood trees make groundwater available to *G. alogus* as dislodged, groundwater-laden leaves (greenfall). We hypothesized that groundwater fluxes mediated by greenfall sustain *G. allogus* through the prolonged dry season and link these aboveground consumers to belowground aquifers.

To test this hypothesis, we first characterized gradients in absolute humidity (air) and water stress in field-collected *G. alogus*. Absolute humidity declined with distance from river across wide stands of floodplain cottonwood forest during the dry season, but not during the rainy season. Similarly, *G. alogus* body water content declined along this gradient. Second, we measured evaporative water loss (EWL) by field-captured *G. alogus* in the laboratory at temperatures bracketing field conditions. EWL ranged from 0.05 ± 0.009 g·individual^{-1}·d^{-1} to 0.13 ± 0.03 g·individual^{-1}·d^{-1} (mean $\pm$ SD, at 30° and 40°C, respectively). These daily losses are high, but still less than the water content of a single cottonwood leaf (0.296 ± 0.124 g H_2O/leaf). Third, we designed field experiments to quantify the relative dependence of *G. alogus* on greenfall. *G. alogus* more frequently consumed greenfall than various controls consisting of dried leaves. This preference occurred in distal habitats and during the dry season, but not proximal to the river or in the rainy season. Finally, we compared estimated daily water fluxes via greenfall to (1) estimates of water demand of the entire *G. alogus* population at our field site, and (2) reports of cottonwood transpiration and San Pedro River base flow from other authors. By our estimates, groundwater fluxes via greenfall sustain *G. alogus* populations despite their trivial magnitude compared to stream discharge and cottonwood transpiration. Primary consumers in turn provide dietary water to higher trophic levels (e.g., abundant and speciose birds in the region) through trophic pathways, thereby fueling secondary production from the bottom up. Thus, riparian trees root animals in the regional water cycle.

Key words: aquifer; desert floodplain; detritivore; greenfall; groundwater; Gryllus alogus; food web; Freemont cottonwood; leaf litter; riparian gallery forest; San Pedro River, Arizona, USA; water cycle.

INTRODUCTION

Freshwater is the key ingredient of life on Earth but is an uncommon commodity in semiarid and arid biomes or during prolonged droughts. Over 75% of freshwater on Earth is ice (Winter et al. 1998) and nearly 99% of unfrozen freshwater is underground (Groundwater Foundation 2008). This groundwater does not go unused. In the United States, drinking water for over 50% of the total population and 90% the rural population is pumped from the ground (National Research Council 2000). Additional groundwater with-

drawals are used for agriculture, in greater amounts than municipal water needs worldwide (Groundwater Foundation 2008). In many U.S. states and other places in the world, groundwater pumping outpaces natural recharge rates and water tables are declining (National Research Council 2000, Glennon 2002). Falling water table levels in turn have led to reduced discharge to surface waters and clear effects on aquatic organisms via diminished habitat quantity and quality (Fleckenstein et al. 2006).

Water table lowering and dampening of peak (flood) flows as a result of dams and water diversions have led to the decline of some notable terrestrial species as well. For example, cottonwood–willow (CWW) forests have declined in many watersheds throughout the western United States (Busch and Smith 1995, Stromberg et al. 1996, Scott et al. 1999, Shafroth et al. 2000, 2002, Webb and Leake 2006), though recent analysis of repeat

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photography suggests a contemporary recovery and increase in CWW and riparian woody vegetation coverage in many southwestern watersheds within the last 50–100 years (Webb et al. 2007). Cottonwood (*Populus* spp.) and willow (*Salix* spp.) are phreatophytes that mine groundwater with deep taproots even when surface flows are immediately accessible (Dawson and Ehleringer 1991, Busch et al. 1992, Snyder and Williams 2000). Declining water tables disconnect these trees from their primary water source, often leading to shifts in forest community structure from CWW forest to dominance by nonnative salt cedar, *Tamarix* spp. (Busch and Smith 1995, Horton et al. 2001, Amlin and Rood 2002, Lite and Stromberg 2005). Plant physiological ecologists routinely link aspects of regional water cycles, variation in water use efficiency at the individual level, and community structure at larger spatial scales. These links are very rarely made in the fields of animal physiology and food web ecology and are relevant to recent advances linking belowground ecosystem processes and aboveground communities (Wardle 2002).

Deserts, arid-land ecosystems, and water webs

Nearly 30 years ago, Noy-Meir summarized the relationship between water, energy, and the structure and function of arid land communities and ecosystems (Noy-Meir 1973, 1974). Specifically, primary and secondary production are limited first by water, not energy, such that desert ecosystems could be characterized by compartment models based on water rather than energy flow (Noy-Meir 1973). Energy limitation may occur seasonally depending on the predictability and timing of rainfall (Noy-Meir 1973, 1974). For example, water limitation may be alleviated on the short-term by concentrated rainfall (e.g., Monsoon season) stimulating primary and secondary production and giving way to energy limitation at higher trophic levels. Finally, behavioral thermoregulation and mobility allow animals to manage heat and water balance more flexibly than plants in space and time (Noy-Meir 1974).

These generalities have several implications for the current study. First, the spatial distribution and temporal windows of appearance of desert plants reflect gradients in water availability in space and time (Stromberg et al. 1993, 1996, Smith et al. 1998, Chesson et al. 2004, Lite and Stromberg 2005, Lite et al. 2005, Stromberg 2007). Second, the arrows in desert food webs should often be interpreted to reflect the magnitude of water fluxes (i.e., a water web), unless atmospheric or surface sources of water are concentrated in space (as a river) or in time (as Monsoon rain). When water resources are concentrated either in space or time, consumers may shift from water- to energy-limitation, and more common food web paradigms in mesic biomes based on energy (Lindeman 1942) or nutrients (Sterner and Elser 2002) may prevail. Third, many desert animals obtain most, if not all of the water they need for maintenance from their diet, as preformed

water from moist food or from metabolic production of water from dry food (Schmidt-Nielsen and Schmidt-Nielsen 1952, Schmidt-Nielsen 1964, Wolf et al. 2002). For example, when dry conditions prevail, animals make foraging decisions about moist food based solely on water stress, water availability, or the water content of food (Golightly and Ohmart 1984; K. E. McCluney and J. L. Sabo, *unpublished data*). Much of this "trophic" water derives ultimately from plants.

In this paper, we quantify the flow of groundwater through desert riparian water webs focusing on the groundwater–plant–primary-consumer link. Riparian phreatophytic plants represent the gateway for groundwater resources to terrestrial consumers living in canopies and at ground level. Thus, in contrast to many ecosystem studies that have focused on water as a delivery mechanism of other materials and especially nutrients (e.g., Pinay et al. 1999, Schade et al. 2002, Valett et al. 2005, Whitledge et al. 2006), we treat water as the resource of interest. Specifically, phreatophytes tap into shallow aquifers to sustain high rates of water use (transpiration) and offset potentially lethal energy loads at the leaf level (Dawson and Ehleringer 1991, Busch et al. 1992, Lambers et al. 1998). The groundwater flux through riparian forests is substantial, especially in semiarid or arid biomes (Devitt et al. 1998, Scott et al. 2000, Kurc and Small 2004, Cleverly et al. 2006). Some of this water is consumed directly by herbivores, either sap suckers or leaf eaters (Andersen 1994, Martinsen et al. 1998), or as high-quality detritus via green (or lower quality yellow), water-laden leaves blown from the forest canopy to the forest floor. Here we focus on the latter: ground-dwelling invertebrates that rely on freshly fallen green leaves ("greenfall") for energy, nutrients, and water.

Thus, the overarching goal of this paper is to root terrestrial riparian animal communities directly in the regional water cycle by quantifying fluxes of groundwater to a key aboveground primary consumer via greenfall from the dominant woody plants in a desert floodplain ecosystem. We evaluate the significance of this small flux to a common riparian detritivore. We then estimate the water demand by whole populations of this primary consumer and compare this to the flux delivered by greenfall as well as more prominent fluxes in regional water budgets (e.g., transpiration and surface discharge). We hypothesize that while greenfall is perhaps a trivial water flux compared to transpiration and the base flow of rivers, the water delivered by greenfall is adequate to sustain whole populations of insect consumers during stressful drought periods. More importantly, we hypothesize that the impact of groundwater on terrestrial animals in riparian zones increases with floodplain width: wide floodplain forests support larger stands of riparian trees and thus provide more spatially extensive water resources than more narrow ribbons of gallery forest.

FIG. 1. Image of the field site showing the San Pedro River near Gray Hawk Ranch, ~2 km south of Charleston Road and the USGS NWISweb Charleston Station (Arizona, USA). The solid line is the San Pedro River, the dashed line is the terrace edge between cottonwood forest on the river floodplain and mesquite bosque.

METHODS AND MATERIALS

Study system: the plants and primary consumers of desert floodplains

We conducted this research in riparian gallery forests occurring in wide floodplains of the upper San Pedro River (hereafter "floodplain gallery forests"; see Fig. 1). The San Pedro River flows north from Sonora, Mexico into southern Arizona, USA. Floodplain gallery forests differ from forests in other reaches of the river that consist mainly of a single band of trees on either side of the river (hereafter, "ribbon gallery forests"). Many of the observations we present below, and all of the experiments took place in a single floodplain gallery forest called Gray Hawk located in Cochise County, Arizona near the township of Sierra Vista (31°36'19.23" N, 110°09'26.44" W). Floodplain gallery forests similar to Gray Hawk are common but irregular features of the upper river; we have active research sites on at least four other similar meanders in a 40-km reach. The San Pedro is one of the last entirely free flowing rivers with perennial reaches in the desert southwest, and is an internationally recognized hotspot of biodiversity. A prominent feature of the upper San Pedro River is extensive coverage by cottonwood–willow (CWW; *Populus fremonti* and *Salix goodingii*) forests, once the most common floodplain forest type in the western United States (Busch and Smith 1995, Stromberg et al. 1996, The Nature Conservancy 2008). CWW forests

along the San Pedro support extremely high abundance and species diversity of birds (over 300 species and an estimated 4 million migrants annually) and mammals (approximately 80 species; TNC 2000). Leaf litter production by cottonwood trees is high and this litter provides a resource and a structural component of habitat for extremely abundant aboveground detritivores, including crickets (*Gryllus alogus*) and isopods (*Porcellio* sp. and *Armadillidium* spp.). Cottonwood leaf litter also serves as an important structural component of habitat for a guild of ground spiders (Lycosidae), an abundant group of predators of early instars and adults of these detritivores. *G. alogus* and at least two species of large lycosid spiders (*Hogna antelucana* and *Arctosa littoralis*) are the numerically dominant invertebrate taxa inhabiting the leaf litter soil layer in floodplain forests (J. L. Sabo, C. U. Soykan, A.C. Keller, and K. E. McCluney, *unpublished manuscript*), and provide an abundant and constant resource for nesting birds (e.g., ground-hawking fly catchers) and several ground-dwelling lizard species (e.g., *Aspidoscelis uniparens*; J. Sabo, *personal observation*). For example, during the dry season of 2003, *G. alogus* accounted for between 15% and 33% of all ground-dwelling invertebrate taxa by abundance in plots with ambient litter (24% ± 5% [mean ± SE]) and between and 30% and 50% of all invertebrate taxa in cleared plots during the dry season (38% ± 6%; J. Sabo, *unpublished data*).

Finally, though surface water is abundantly available at the river's edge, the scale of wide floodplains is large enough (Fig. 1) to inhibit regular commuting by small-bodied ground-dwelling invertebrates (like *G. alogus*) from distal portions of floodplains to the river for drinking. In these "distal" habitats, the only available water for primary consumers occupying the forest floor is through living plant material: greenfall, herbaceous plants, and grasses (e.g., *Brickellia* spp., *Sorghum halepense*, and others). We have many direct observations of *G. alogus* consuming freshly fallen cottonwood leaves (as well as dry litter material). Greenfall of other species is rare, but brown cottonwood litter from the previous year is ubiquitous. We hypothesized that (1) *G. alogus* is water stressed in distal, but not near-river ("proximal") portions of floodplain gallery forests, (2) *G. alogus* seeks out cottonwood greenfall in response to its high relative water content, and (3) *G. alogus* can mitigate high water stress in distal habitats by consuming greenfall, and that the water flux associated with greenfall is adequate to sustain *G. alogus* populations at high density without surface water.

Overview of methods

The goals of this paper are threefold, and the methods that accompany each goal are notably different. First we rely on field observations of climate and the condition of *G. alogus* to quantify gradients in water stress. Thus, we measured air temperature and absolute humidity (AH) in replicated near-river and distal portions of a single floodplain gallery forest. We predicted that distal portions of floodplain gallery forests would have lower absolute humidity and more severe fluctuations in temperature (indexed by higher maximum and lower minimum temperatures). We further predicted that these differences would vanish during the summer monsoon season when soils are saturated by rains and air temperatures are more buffered against severe fluctuations by higher absolute humidity. In addition to quantifying gradients in physical conditions, we also measured the water content (as g H_2O per g dry mass, following Hadley [1994]) of *G. alogus* in these habitats to compare the hydric state of this animal along this hypothetical gradient in physical conditions and surface water availability. We predicted that *G. alogus* would have lower body water content in distal relative to near-river portions of floodplain gallery forests reflecting water limitation in the former but not the latter.

Second, we present a field experiment designed to evaluate if *G. alogus* seeks out greenfall to alleviate this water limitation. Specifically, we designed an in situ cafeteria experiment in which we experimentally added several types of naturally occurring leaves: fresh, experimentally dried, and naturally abscised leaves of up to three species. These leaf additions were carried out in replicated plots in habitats with and without river access to measure the relative dependence of *G. alogus* on greenfall as a water source. We executed this

experiment in both the dry and rainy (monsoon) seasons when surface water gradients were strong and weak, respectively. We predicted that *G. alogus* would seek out greenfall in distal, but not near-river habitats and that these differences would all but disappear between the dry and monsoon seasons, reflecting foraging decisions based on water limitation on the part of *G. alogus*.

Third, we use gravimetric analyses of water loss, a classic method in insect physiology, to quantify the daily water requirements of *G. alogus* under a variety of conditions that bracket field conditions. Simultaneously, we quantified the water flux from aquifers to the forest floor via greenfall on a grams per square meter per day basis. The latter was done by counting greenfall in replicated cleared plots (checked hourly) and by measuring the water content of greenfall collected in situ. Finally, we measured *G. alogus* activity abundance in the same cleared plots (as above) in order to quantify total population-level water demand by this species on a grams per square meter per day basis. We predicted that the water flux represented by greenfall, though trivial compared to cottonwood evapotranspiration and other more prominent ecosystem-level fluxes, is adequate to sustain the current population size of *G. alogus* under field conditions during the dry season.

Field measurement of physical gradients

We measured the air temperature and relative humidity in replicated plots, three each in near-river and distal habitats within a single floodplain gallery forest (Gray Hawk) as well as on the terrace immediately above the distal edge of the floodplain. All measurements were made continuously every 5 minutes over a five-day period in the dry season (26–30 June 2006) and monsoon season (6–10 September 2006) using Hobo micro-station data loggers equipped with Temp/RH smart sensors (Onset, Bourne, Massachusetts, USA) housed in $15 \times 21 \times 19$ cm white, plastic, ventilated, radiation shields. All probes were hung at 1 m from the ground surface. During the monsoon season, high flows in side channels precluded deployment of climate stations to distal habitats, thus we report differences between near-river and terrace stations only for this season. In both seasons, we report differences among habitat types (three dry season, two monsoon season) as average minima or maxima across the five-day measurement interval (where values are averaged across five days and three replicate sites, but standard errors are based only on variation among sites).

We calculated absolute humidity from relative humidity and temperature measured on site assuming a partial pressure of H_2O based on the elevation at our field site. To test the statistical significance of differences in temperature and air humidity extremes (minimum and maximum) we used F ratios to test the equal variance assumption followed by either two-sample t tests assuming equal variance (homoscedasticity) or unequal variance (heteroscedasticity). In all of these

tests, we predicted decreases in minimum and maximum AH and increases in minimum and maximum temperature with distance from river. Thus, we use one-tailed probabilities for all t tests; however, we correct these P values for multiple tests (two seasons) to avoid experiment-wide type-I error inflation using the Bonferroni method (e.g., one-tailed $P_{crit} = 0.05/2 = 0.025$).

Field measurement of cricket body water

We estimated total body water content for a sample of crickets at Gray Hawk and a second floodplain gallery forest (Boquillas) in near-river ($N = 10$) and distal ($N = 18$) habitats during the dry season of 2004 (7–15 July 2004). *G. alogus* were captured by hand and frozen in air tight vials within several hours of capture. Water from these animals was extracted via cryogenic vacuum distillation and water weights and dry weights were recorded at Stable Isotope Ratio Facility for Environmental Research (SIRFER, University of Utah, Salt Lake City, Utah, USA). To test the statistical significance of differences in total body water content between near-river and distal samples, we used a two-sample t test after checking for the equality of variances with an F test of the ratio of variances ($F_{5,5} = 1.01$, $P > 0.9$).

Field experiments

We designed an in situ cafeteria experiment in which leaves of different hypothesized chemical composition and water content were experimentally added to replicated plots in near-river and distal gallery forest habitats. Specifically, we added three replicate sets of the following leaves to each of three plots in each habitat type (near-river and distal): freshly collected cottonwood (*Populus fremontii*) refrigerated to maintain water content ("wet green"), freshly collected, sun-dried cottonwood ("dry green"), dry brown but intact cottonwood collected from the forest floor ("dry brown"), freshly collected willow (*Salix gooddingii*; "wet willow"), and freshly collected seep willow, (*Baccharis glutinosa*; "wet *Baccharis*"), similarly refrigerated to maintain water content. Leaves (one of each, five total) were attached to 2×12 cm door shims using rubber bands in the late afternoon (15:00 hours). To minimize the influence of individual variation in plant tissue chemistry on cricket foraging decisions, all fresh leaves were collected consistently from the same trees (five or six for each species) located in the distal part of the floodplain gallery forest. These shims were kept at ~15°C until dusk (~18:00 hours), at which time we deployed three shims in each of the six plots. The following morning (~07:00 hours) we returned to the plots and enumerated the number of each type of leaf attacked (out of three possible per site) and estimated the percentage of each leaf type consumed (increments of 5%, 0–100%). For the remainder of this paper, we refer to these two response variables as "percentage of attacks" (as a percentage, based on the number attacked of nine total) and "percentage consumption" (as a

percentage of total area consumed), and analyze them separately. To verify that observed attacks on leaves were the work of *G. alogus*, we made ~40 hours of direct observations of leaves attached to shims (J. L. Sabo and L. Thompson, *unpublished data*). In all of these observations, *G. allogus* was the only consumer of experimental leaves, and was observed commonly on green cottonwood leaves. However, it is possible that other arthropods and even mammals may have uncommonly contributed to leaf consumption.

We conducted this experiment in four "runs," each consisting of three consecutive nights during either the dry or monsoon seasons of 2005 and 2006 (8–10 June and 16–18 September 2005; 16–18 June and 15–17 August 2006: dry and monsoon season, respectively). For analysis, we pooled observations at each site within a single run (e.g., nine shims per site per run). After pooling these observations, we calculated the percentage of "attacks" (p) on various leaves by *G. alogus* as $p = (a/3) \times 100$, where a is the number of leaves of a specific type showing positive evidence of consumption in a given run out of three (four possible percentages = 0, 33, 66, and 100%). These percentages were averaged across the nine replicates per run. We also calculated the percentage of total available leaf consumed as the average percentage within a run for a given leaf type (e.g., $n = 9$).

Statistical analysis of experimental results.—The design of this experiment is complex. Ideally, one would analyze this experiment using an omnibus test that captures the two fixed factors of interest (leaf types, with five levels, location within the floodplain, with two levels) as well as the two repeated measures (season and year, with two levels each). Moreover, one could account for the nesting of the plots (random effect) within location (fixed effect). Here we simplify this design to increase statistical power and reduce model complexity by analyzing the data as if they were performed as four separate experiments in time (dry and monsoon seasons of 2005 and 2006). Thus, for each of these four experiments, we analyzed our data as a split-plot design where the factors were leaf type (fresh cottonwood, dry green cottonwood, dry abscised cottonwood, fresh willow, fresh seep willow) and location in the floodplain (near-river/distal), and plot as a random factor nested within location. We then use Bonferroni-corrected P values (critical $\alpha = 0.05/4 = 0.0125$) to avoid spurious rejection of null hypotheses resulting from experiment-wide type-I error inflation (four rather than one omnibus tests). This simplification precludes estimation of temporal effects.

In addition to the complexity of our experimental design, our responses (percentage of attacks, percentage consumption) exhibited strong departures from the equal variance assumption of parametric methods. Since nonparametric procedures for multifactor designs are few and far between (Zar 1998), we resorted to permutation techniques to estimate exact probabilities

for various effects (location, leaf type) and contrasts (greenfall vs. other leaves). ANOVA via permutation was conducted using the programs PERMVAR and PERMANOVA (*available online*).[3]

Lab experiments

We estimated the daily water requirements of field-captured *G. alogus* by measuring evaporative water loss (EWL, in g/h) under laboratory conditions using gravimetric techniques. We collected several hundred adult *G. alogus* in the spring of 2006. These crickets were housed in a captive breeding facility on campus at Arizona State University at approximately 30°C and ambient (i.e., low) humidity. We measured water loss in male and female adult crickets at 30° and 40°C under conditions of ~0% absolute humidity. In each experiment, crickets were housed individually in 20-dram (79.394-mL) plastic vials on a test tube rack which was in turn housed within an airtight acrylic dessicator cabinet. Zero humidity was maintained by placing tubes (constructed with nylon stockings) of Drierite (W. A. Hammond Drierite Company, Xenia, Ohio, USA) in the dessicator. Temperature (constant 30° or 40°C) was maintained by a Conviron model EF7 incubator (Controlled Environments, Inc., Pembina, North Dakota, USA) with a 12 hour on, 12 hour off simulated photoperiod. Crickets were weighed every three hours until death (or for <48 hours at 40°C and ~5 days at 30°C) on a Mettler-Toledo XP205 Deltarange microbalance (Mettler-Toledo, Columbus, Ohio, USA) with 0.01-mg precision. We then measured the dry mass of all individuals by drying insects to a constant mass at 65°C. Total water content was measured as the difference between initial and final dry mass. Cumulative water loss was estimated by the difference between live mass at time t (m_t) and the initial live mass (m_0) and the instantaneous rate of water loss can be expressed as ($m_{t+\tau} - m_t$)/τ, where τ is the time elapsed (in minutes) between measurements.

H_2O fluxes through greenfall and cricket populations at the ecosystem level

We estimated the *maximum* water flux associated with greenfall at the ecosystem level (in $g \cdot d^{-1} \cdot m^{-2}$) by measuring the greenfall rate (G) and the average water content (WC) of a sample of freshly picked cottonwood leaves from our study site (simulating a freshly fallen leaf). Here, freshly picked leaves simulate fresh greenfall with the highest possible water content and allow us to estimate the maximum water flux from this source. Greenfall rates were estimated by counting freshly fallen leaves in cleared 2 × 25 m plots at Gray Hawk. Briefly, we cleared four plots (two near the river and two in a distal portion of the floodplain at Gray Hawk) and scanned, counted, and removed all greenfall (fresh green and yellow leaves) every two hours over a single 24-hour

period in early July 2006. We chose this single 24-hour period to be a representative day in terms of wind conditions for the dry season (calm morning, gusty afternoon, calm evening). The water flux (F) associated with greenfall was then estimated as the product $G \times$ WC. Similarly, we estimated the total water demand of crickets at the ecosystem scale (i.e., WD in $g \cdot m^{-2} \cdot d^{-1}$) as the product of cricket density, D (i.e., in individuals/m^2) and individual water demand estimated as evaporative water loss, EWL (i.e., in $g \cdot individual^{-1} \cdot d^{-1}$) at a given temperature. We estimated cricket density on the same cleared plots used for greenfall rate determination by walking 25-m transects along the center line of the plots once every two hours for a 24-hour period. Cricket density is reported as the maximum number of crickets observed in a single transect over this 24-hour period. We chose this method rather than more traditional Winkler extractions of invertebrates from litter because we have consistently observed that *G. alogus* seek clumped shelter in patches of deep litter by day, making it difficult to collect these large mobile crickets in Winkler bags and making day-time collections unlikely to be representative samples. At night, crickets disperse across forest floor habitats with and without litter, making nighttime visual transects preferable (J. Sabo, *personal observation*). Moreover, data from pitfall traps in association with a large scale litter removal experiments at the same site (J. L. Sabo, C. U. Soykan, A. C. Keller, and K. E. McCluney, *unpublished manuscript*) indicate a preference of *G. alogus* for litter-free habitats (similar to our cleared transect plots). Nevertheless, visual surveys likely yield an underestimate of true (vs. activity) abundance. We elaborate on the implications of this assumption in the *Discussion*. Finally, we estimated the total amount of groundwater consumed by crickets via consumption of greenfall (GWC) as the product of average greenfall water content (WC) and the percentage of greenfall consumed (PC) by crickets during the 2006 greenfall addition experiments. Here, percent leaf consumption was calculated as an average across replicates in distal habitats. A more complete description of these calculations and error propagation equations is given in Appendix A.

Estimating representative fluxes in the regional water cycle

For comparison of water fluxes via greenfall to more regional fluxes, we used transpiration estimates from sap flow measurements made on cottonwood trees on the San Pedro River near our field sites (Schaeffer et al. 2000, Gazal et al. 2006, Williams et al. 2006). Here we averaged stand-level transpiration values from intermittent and permanent sites (Williams et al. 2006). Surface water fluxes were calculated as the average total daily discharge (in g/d) averaged over the entire record during the month of May of 2006 and 2007 at the Charleston station (U.S. Geological Survey, NWISweb station #09471000).

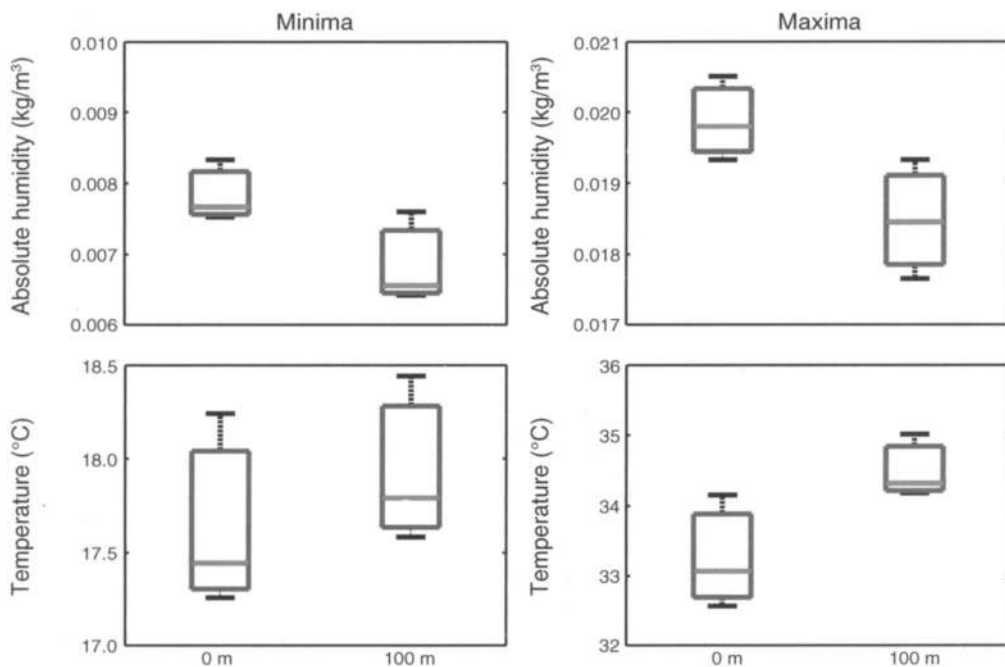[3] ⟨http://www.stat.auckland.ac.nz/~mja/Programs.htm⟩

FIG. 2. Climate gradients during the dry season in floodplain gallery forests on the San Pedro River (Arizona, USA). Minimum and maximum daily absolute humidity and shaded air temperature in near-river (0 m) and distal (100 m) floodplain habitats. Center bar, box, and whiskers indicate median, inner quartile, and 95% of the data. Note the different scales for minima and maxima.

RESULTS

Physical gradients

Absolute humidity was significantly lower (measured as either minimum or maximum AH) in distal vs. near-river habitats during the dry season, reflecting decreasing riverine influence on AH across the riparian CWW gallery forest (Fig. 2, Table 1). Maximum air temperatures were significantly higher in distal vs. near-river habitats during the dry season (Fig. 2), but minimum air temperatures were not statistically different in these two habitats (Table 1). These patterns were reversed in the wet season. Absolute humidity was not significantly different in distal vs. near-river habitats (Fig. 3, Table 1) reflecting the influence of atmospheric sources of air moisture and weaker influence of the river across the river to upland gradient. By contrast, minimum air temperatures were significantly higher near the river (Fig. 3, Table 1), whereas maximum air temperatures were higher in distal habitats. Thus, during the dry season, distal habitats are both warmer by day and present considerably lower absolute humidity than habitats close to the river.

TABLE 1. Summary of statistical analyses of microclimate gradients along the San Pedro River, southeast Arizona, USA.

Measure	0 m from river	100 m from river	t	df	P†
Dry season					
Min AH	0.0078 (1.7×10^{-7})	0.0069 (4.13×10^{-7})	3.09	4	0.018
Max AH	0.0199 (3.6×10^{-7})	0.0185 (7.23×10^{-7})	3.29	4	0.015
Min temp	17.65 (0.27)	17.94 (0.2)	−1.04	4	0.18
Max temp	33.26 (0.67)	34.5 (0.2)	−3.28	4	0.015
Wet season					
Min AH	0.014 (3.7×10^{-7})	0.0135 (1.63×10^{-7})	1.68	4	0.18
Max AH	0.02 (4.3×10^{-7})	0.0216 (6.33×10^{-8})	1.74	4	0.2
Min temp	13.83 (0.051)	13.19 (0.051)	4.92	4	0.02
Max temp	26.34 (0)	28.31 (0.16)	−8.62	2‡	0.007

Notes: Mean values (and SD in parentheses) are for sites at 0 m and 100 m from the river. Student's t tests evaluated hypothesized changes in minimum (Min) and maximum (Max) daily values for absolute humidity (AH, in g H_2O/g air) and temperature (Temp, in °C) during May (dry season) and September (wet season).

† One-tailed Bonferroni critical values are 0.025 for two (seasonal) tests per response variable.

‡ Degrees of freedom adjusted for unequal variance; t, and P values reflect t test assuming unequal variance.
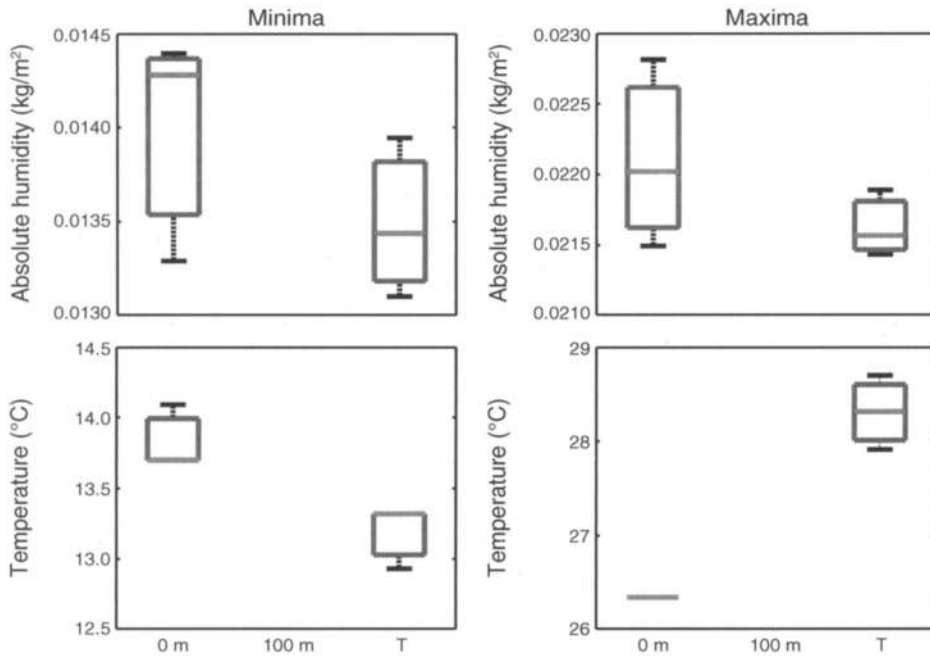
Fig. 3. Climate gradients during the monsoon season in floodplain gallery forests on the San Pedro River. Minimum and maximum daily absolute humidity and shaded air temperature in near river (0 m) and distal floodplain habitats. Here, distal measurements are from the terrace (T) above the inundated floodplain ~125 m from river's edge. Center bar, box, and whiskers indicate median, inner quartile, and the range containing 95% of the data. Note the different scales for minima and maxima.

Cricket body water

Cricket body water content was 25% higher in near-river vs. distal habitats (Fig. 4; distal = 2.99 ± 0.24 g H_2O/g dry mass; near-river = 3.73 ± 0.254 g H_2O/g dry mass [mean ± SE]; $n = 6$ for each group) and these differences were significant ($t = -3.04$, df = 10, $P = 0.013$). This result suggests that water balance at the individual level is more difficult to maintain far from surface water during the dry season and that G. alogus is water stressed in distal portions of floodplain forest ecosystems.

Experimental leaf additions

During the dry season of both years, percentage of attacks and consumption were higher for field-collected, fresh (wet green) cottonwood leaves than abscised (dry brown) or experimentally sun-dried (dry green) cottonwood leaves (Figs. 5 and 6). This pattern was stronger in distal habitats than in near-river habitats, as evidenced by significant distance × leaf interactions for attacks (2005 dry season; Table 2) and consumption (2006 dry season; Table 3). Average water content of CWW leaf tissue as well as leaf size and thus total water content are higher in cottonwood leaves, whereas C:N is typically lowest for willow leaves (Fig. 7). Moreover, Baccharis plants were more covered with a sticky exudate and more heavily attacked by herbivores than willow leaves in 2005; this phenomenon was not observed in 2006 (J. Sabo, personal observation)

Percentage of attacks and consumption of any leaf species were notably lower in the wet vs. dry season of both years (Figs. 5 and 6). Percentage of attacks and consumption were both near zero for all five leaf types during both wet seasons. However, because we opted not to include season or year as an effect in our analysis, we cannot compare these patterns statistically. Nevertheless the patterns are strong; percentage of attacks and consumption are near zero for all types of leaves regardless of location in the floodplain in both wet seasons, whereas percentage of attacks and consumption of wet leaves are greater than zero during both dry seasons and higher in distal vs. near-river habitats.
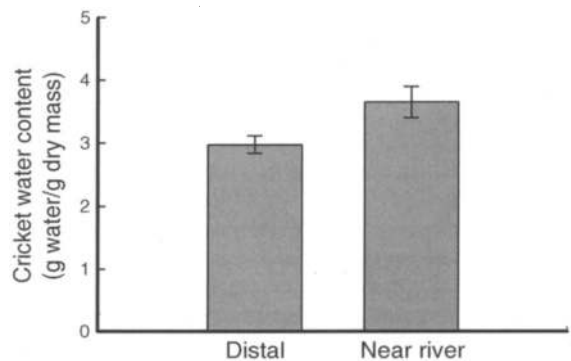

Fig. 4. Water content of the cricket Gryllus alogus in distal and near-river gallery forests at Gray Hawk, Cochise County, Arizona, USA. Bars show means ± SE.
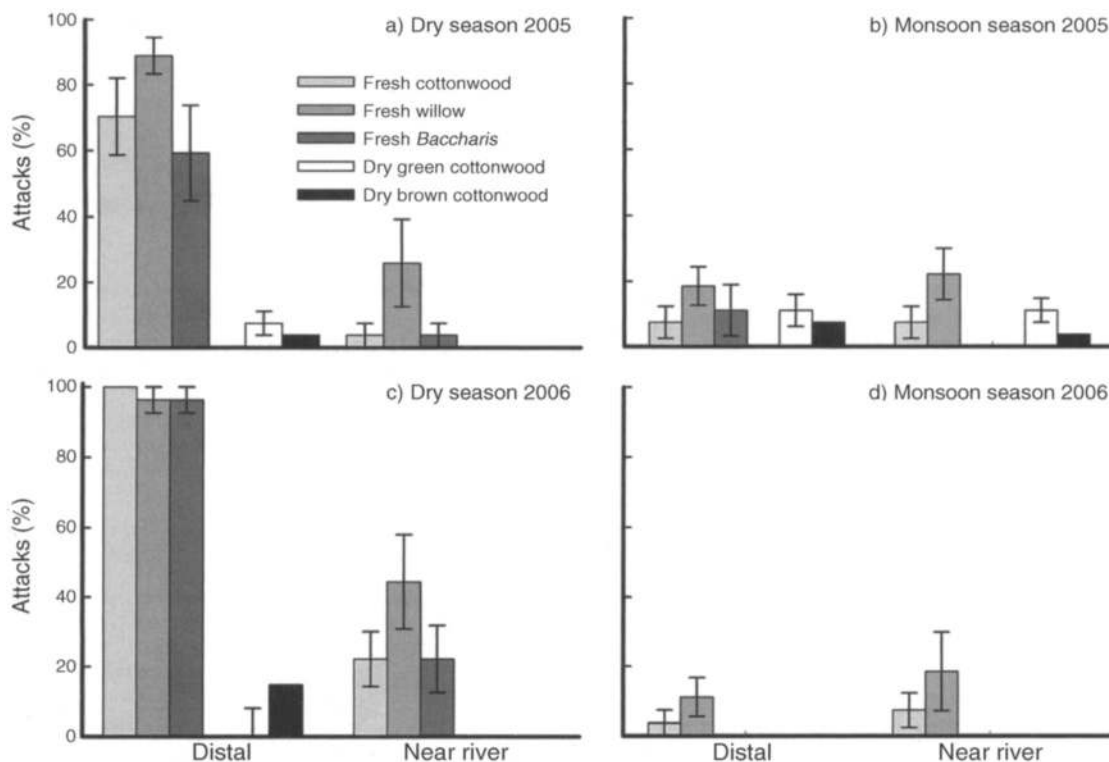
FIG. 5. Percentage of attacks, mostly by *G. alogus*, on five types of simulated greenfall: fresh cottonwood, willow, seep willow (*Baccharis*), sundried green cottonwood, and brown cottonwood (litter). Panels show results from repeated experimental runs during the dry and monsoon seasons of 2005 and 2006 in distal and near-river gallery forests. Bars represent means ± SE. Percentages of attacks were measured as $(a/3) \times 100$, where a is the number of a given leaf type with positive evidence of herbivory out of three possible leaves in each replicate (three plots on each of three sequential nights at each distance = 9 replicates).

When leaf × distance interactions were nonsignificant during the dry season (e.g., 2005 attack rate and 2006 consumption), distance effects alone were significant or marginally so (Tables 2 and 3). This result suggests that during the dry season detritivores either seek out more water-laden leaves (significant interaction) or that wet leaves are not a preferred resource when free water is more plentiful (e.g., near-river). Leaf × distance effects were extremely low and nonsignificant during both wet seasons. This finding, combined with overall low percentage of attacks and consumption of any leaves during the monsoon, suggests that litter and greenfall are less important resources for detritivores during the wet season.

Leaf C:N and water content

The nitrogen content by atoms was highest (lowest C:N) for freshly picked willow leaves and lowest (high C:N) for freshly picked cottonwood leaves (Fig. 7). Differences among leaves in C:N were highly significant ($H = 47.14$, $n = 68$, $P < 0.001$). Water content at first appeared lowest for freshly picked cottonwood leaves and highest for seep willow (Fig. 7), but was not significantly different ($H = 5.06$, $N = 6$, $P = 0.08$). By contrast, water content was more than three times

higher for cottonwood greenfall than willow greenfall (Fig. 7; t test assuming unequal variance: $t = 3.93$, df = 3, $P = 0.03$). Finally, cottonwood leaves are on average the largest in terms of dry mass (cottonwood, 0.15 ± 0.02 g; willow, 0.06 ± 0.004 g; and seep willow, 0.07 ± 0.005 g). In summary, though cottonwood leaves have lower initial water content they appear to maintain higher internal water content as litter, longer than other leaves examined in this study, and they deliver more total water per leaf (cottonwood, 0.29 ± 0.03 g; willow, 0.11 ± 0.008 g; and seep willow, 0.14 ± 0.005 g).

Gravimetric determination of EWL for G. alogus

G. alogus survival was low at 40°C, ~67% only 24 hours after the start of the experiment. At 30°C, all animals survived 24 hours and we observed ~92% survival 122 hours after the start of the experiment. During the dry season at our field sites, average daily maximum surface soil temperatures (5 cm depth) exceed 30°C from mid-May to the onset of monsoon rains in mid-July. Average daily maximum temperatures of soil at this depth are between 30° and 40°C from June to the onset of monsoon rains. Temperature extremes are slightly dampened by leaf litter cover, where crickets seek refuge for most of the day (Y. Marusenko and J. L.
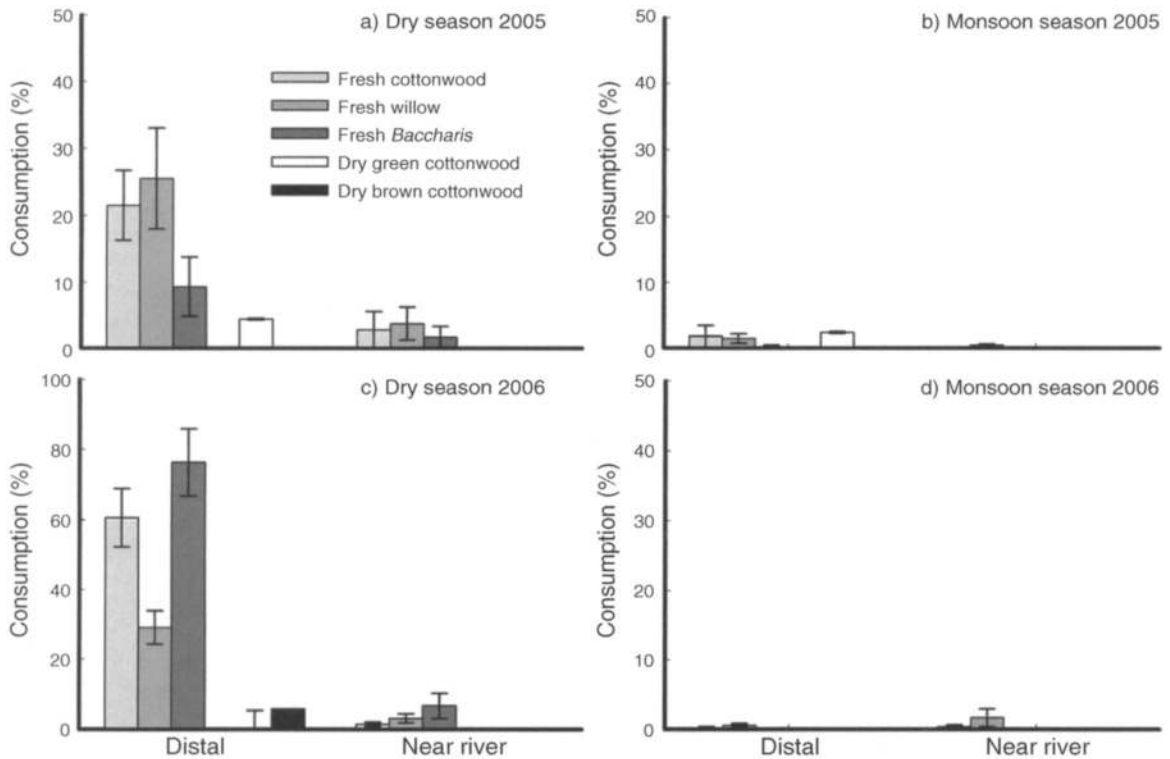
Fig. 6. Percentage consumption, mostly by *G. alogus*, of five types of simulated greenfall: fresh cottonwood, willow, seep willow (*Baccharis*), sundried green cottonwood, and brown cottonwood (litter). Panels show results from repeated experimental runs during the dry and monsoon seasons of 2005 and 2006 in distal and near-river gallery forests. Bars represent means ± SE. Percentage consumption was estimated for each leaf (three per replicate) in increments of 5% (0–100%), leading to an average percentage consumption value within each replicate (three plots on each of three sequential nights at each distance = 9 replicates). Standard errors are then based on the average of within-replicate average percentage consumption values (e.g., $n = 9$).

Sabo, *unpublished manuscript*; J. L. Sabo, C. U. Soykan, A.C. Keller, and K. E. McCluney, *unpublished manuscript*). Nevertheless, our results from the lab suggest that exposure to the highest field temperatures (~40°C) leads to significant water loss that is not sustainable beyond 24 hours without access to water through trophic or free sources.

Hourly EWL was significantly higher (average of first 24 hours) at 40°C than at 30°C (Fig. 8; EWL at 30°C, $1.94 \times 10^{-3} \pm 7.89 \times 10^{-5}$ g/h; EWL at 40°C, $5.24 \times 10^{-3} \pm 3.98 \times 10^{-4}$ g/h [mean ± SE]; *t* test assuming unequal variance, $t = -7.1$; df = 19; $P < 0.001$). Daily cumulative losses were also significantly different between temperatures (daily cumulative EWL at 30°C = 0.046 ± 1.97 × 10^{-3} g; daily cumulative EWL at 40°C = 0.114 ± 9.55 × 10^{-3} g; *t* test assuming unequal variance, $t = -6.93$; df = 20; $P < 0.001$).

On average, evaporative water loss comprised 10.9% ± 0.47% (mean ± SE) of starting wet mass at 30°C and 27.9% ± 2.68% of starting wet mass at 40°C after one day of exposure to the respective temperature treatment. These losses translate into final water contents of 2.66 ± 0.176 g water/g dry mass at 30°C and 1.55 ± 0.19 g water/g dry mass at 40°C.

Comparison of water fluxes: greenfall and total population water demand for G. alogus

The total water flux from aquifers to the forest floor via greenfall (FL) at Gray Hawk is ~0.14 ± 0.025 g $H_2O \cdot m^{-2} \cdot d^{-1}$ (Table 4). This water flux is small compared to estimates of transpiration for cottonwood trees in nearby CWW gallery forests on the same river (range: 6500–14 700 g $H_2O \cdot m^{-2} \cdot d^{-1}$) and even smaller when compared to the average discharge of the San Pedro River during the month of May (6.9 × 10^9 g H_2O/d; Table 4).

We then scaled EWL estimates from the lab to a population-level EWL based on census data for the density of *G. alogus*. The total water demand of the entire population of *G. alogus* on the same plots in which greenfall fluxes were measured ranges from 0.0395 ± 0.005 to 0.11 ± 0.012 g $H_2O \cdot m^{-2} \cdot d^{-1}$ (at 30° and 40°C, respectively) assuming that lab estimates of EWL prevail in the field.

Despite the trivial magnitude of the greenfall water flux, water supply by greenfall appears to be sufficient to support populations of this abundant consumer even under very stressful conditions (40°C and ~0% absolute humidity). Our preliminary results suggest that the litter

TABLE 2. Summary of statistical analyses of the proportion of attacks (no. attacks/4) on five different leaf types in near-river and distal habitats ($n = 9$ replicates for each leaf type in each habitat).

Effect	df	SS	MS	Pseudo-F	Permutation P	Monte Carlo P
Dry season 2005						
Distance	1	51 797.5	51 797.5	77.03	0.001	0.001
Distance(plot)	4	2689.88	672.5			
Leaf	4	49 911.1	12 477.8	16.15	0.001	0.001
Leaf × distance	4	17 118.5	4279.6	5.54	0.003	0.002
Leaf × plot	16	12 360.7	772.5			
Total	89	211 044.4				
Dry season 2006						
Distance	1	28 889.6	28 889.63	4.37	0.1	0.086
Distance(plot)	4	26 414.3	6603.58			
Leaf	4	104 714.32	26 178.58	16.49	0.001	0.001
Leaf × distance	4	12 670.86	3167.7	1.99	0.13	0.13
Leaf × plot	16	25 402.96	1587.69			
Total	89	234 447.65				
Wet season 2005						
Distance	1	1000.0	1000.0	0.18	0.69	0.69
Distance(plot)	4	22 123.46	5530.86			
Leaf	4	22 172.84	5543.21	4.44	0.015	0.01
Leaf × distance	4	1777.78	444.4	0.36	0.85	0.84
Leaf × plot	16	19 975.31	1248.46			
Total	89	181 123.46				
Wet season 2006						
Distance	1	111.1	111.1	0.2	0.69	0.7
Distance(plot)	4	2277. 8	569.4			
Leaf	4	15 527.8	3881.9	6.62	0.002	0.001
Leaf × distance	4	583.3	145.8	0.25	0.92	0.92
Leaf × plot	16	9388.9	586.8			
Total	89	81 222.2				

TABLE 3. Summary of statistical analyses of the average percentage consumption (0–100%) by crickets for five different leaf types (dry brown, dry green cottonwood, fresh green cottonwood, willow, and seep willow) in near-river and distal habitats ($n = 9$ replicates for each leaf type in each habitat).

| Effect	df	SS	MS	Pseudo-F	Permutation P	Monte Carlo P
Dry season 2005						
Distance	1	43 867.04	43 867.04	35.4	0.001	0.001
Distance(plot)	4	4955.1	1238.78			
Leaf	4	44 727.48	11 181.87	7.48	0.001	0.001
Leaf × distance	4	16 305.4	4076.35	2.73	0.034	0.028
Leaf × plot	16	23 920.18418	1495.01			
Total	89	225 232.67				
Dry season 2006						
Distance	1	40 056.17	40 056.17	6.21	0.027	0.018
Distance(plot)	4	25 818.84	6454.71			
Leaf	4	95 333.36	23 833.34	12.44	0.001	0.001
Leaf × distance	4	26 602.12	6650.53	3.47	0.007	0.006
Leaf × plot	16	30 647.23	1915.45			
Total	89	270 634.56				
Wet season 2005						
Distance	1	605.36	605.36	0.35	0.1	0.64
Distance(plot)	4	6944.3	1736.08			
Leaf	4	19 981.39	4995.35	4.06	0.013	0.006
Leaf × distance	4	2303.83	575.96	0.47	0.82	0.79
Leaf × plot	16	19 687.72	1230.48			
Total	89	160 485.87				
Wet season 2006						
Distance	1	111.1	111.1	0.189	0.75	
Distance(plot)	4	2347.22	586.81			
Leaf	4	14 937.5	3734.38	5.97	0.002	
Leaf × distance	4	756.94	189.24	0.3	0.91	
Leaf × plot	16	10 013.89	625.89			
Total	89	81 500.0				
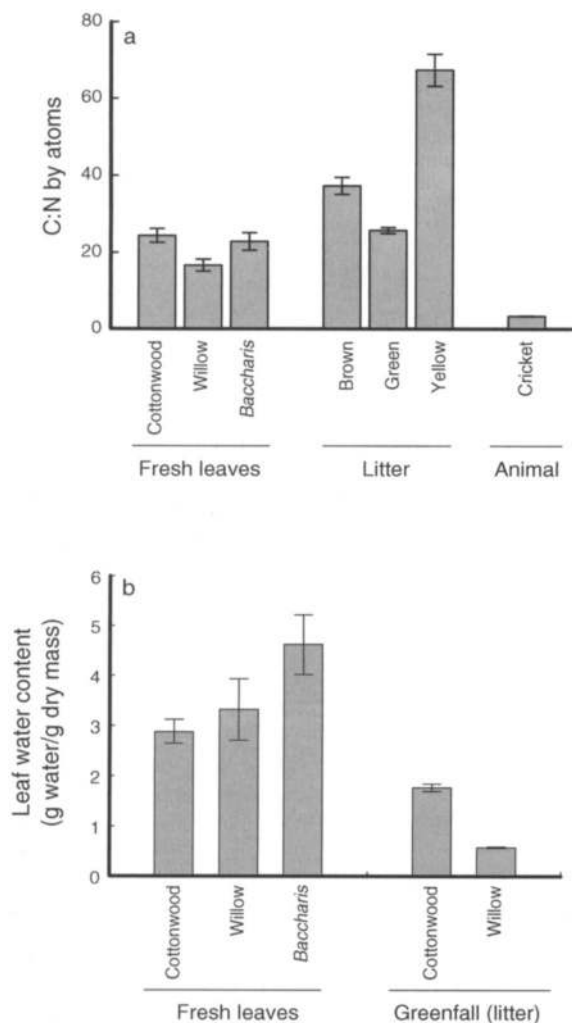
FIG. 7. (a) The carbon-to-nitrogen ratio of freshly picked leaves (cottonwood, willow, and seep willow [*Baccharis*]), litter (green, yellow, and brown cottonwood litter), and crickets (*G. alogus*). (b) The water content of freshly picked leaves from the gallery forest at Gray Hawk (cottonwood, willow, and seep willow) and of greenfall collected directly from the forest floor (cottonwood and willow only). Bars represent means ± SE.

environment provides conditions at slightly higher (e.g., nonzero) AH and lower average temperature (Y. Marusenko and J. L. Sabo, *unpublished manuscript*). Thus, behavioral thermoregulation made possible by the dry litter layer coupled with groundwater supplied by greenfall, allow a water-limited consumer to persist at high density far from surface water in desert riparian floodplain forests.

DISCUSSION

Deserts comprise over one-third of the Earth's terrestrial surface (Schlesinger et al. 1990) and water is the paramount resource in these arid landscapes (Noy-Meir 1973). Rivers create riparian oases in these

landscapes, where surface flow and near-surface aquifers lend to more concentrated and abundant sources of water for direct and indirect consumption by plants and animals. None of these observations are particularly novel for plant ecologists; it is well known that depth to groundwater and river discharge have strong effects on desert plant assemblages (Auble et al. 1994, Busch and Smith 1995, Shafroth et al. 2000, Friedman and Lee 2002, Shafroth et al. 2002, Lite and Stromberg 2005, Stromberg et al. 2007a, b). Moreover, many of the core concepts in ecosystem ecology are based on scaling water use by individual plants to larger spatial scales (Ehleringer and Field 1993, Lambers et al. 1998, Hetherington and Woodward 2003, Huxman et al. 2004). Plants are a critical component of a regional water cycle, linking aquifers to the atmosphere via transpiration. This landscape perspective has not taken hold in animal ecology despite the overwhelming importance of water balance in the study of animal physiological ecology (e.g., Nagy 1972, Nagy et al. 1976, 1991, Nagy and Costa 1980, Nagy and Petersen 1988, Walsberg 2000, Tracy and Walsberg 2001, 2002, Wolf et al. 2002). Though most animals may not have significant
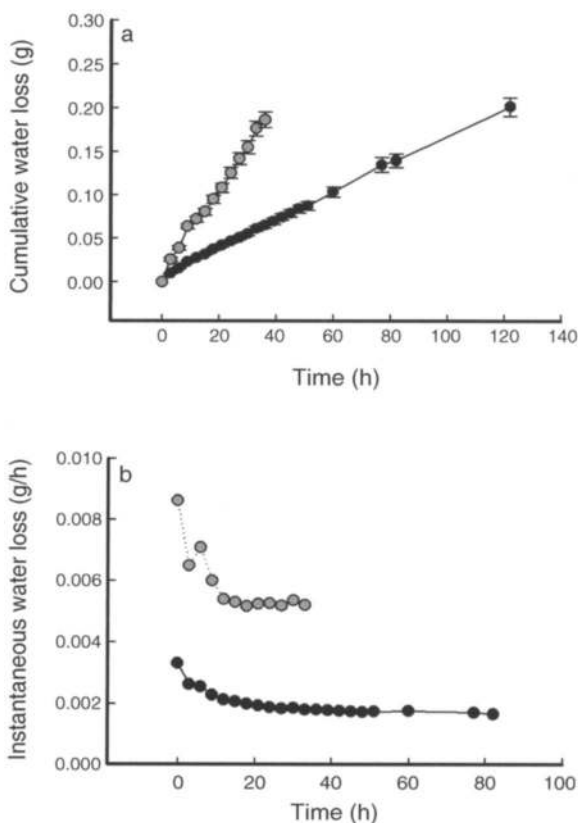

FIG. 8. (a) Cumulative and (b) instantaneous water loss by *G. alogus* in laboratory water stress trials at 30°C (black circles) and 40°C (gray circles), which bracket field temperatures in the gallery forest at Gray Hawk.

TABLE 4. Comparison of water fluxes between the subsurface aquifer and forest floor via greenfall, and between greenfall and cricket populations inhabiting distal floodplain gallery forests along the San Pedro River, southeast Arizona, USA.

Variable	Units	N	Mean	SD
Greenfall rate (G)	no. leaves·m^{-2}·d^{-1}	4	0.48	0.14
Greenfall water content (WC)†	g H_2O/leaf	3	0.291	0.177
Estimated water flux from aquifers to forest floor via greenfall ($F = G \times$ WC)	g H_2O·m^{-2}·d^{-1}	NA	0.14	0.025
Resting water demand by crickets (EWL) at 30°C‡	g H_2O·cricket^{-1}·d^{-1}	24	0.047	0.01
Cricket density (D)§	no. crickets/m^2	2	0.85	0.49
Estimated daily water demand for cricket population at 30°C ($I = D \times$ EWL)	g H_2O·m^{-2}·d^{-1}	NA	0.04	0.005
Resting water demand by crickets (EWL) at 40°C‡	g H_2O·cricket^{-1}·d^{-1}	24	0.126	0.025
Cricket density (D)§	no. crickets/m^2	2	0.85	0.495
Estimated daily water demand for cricket population at 40°C ($I = D \times$ EWL)	g H_2O·m^{-2}·d^{-1}	NA	0.107	0.0124
Proportion of cottonwood leaves consumed (PC)¶	no. leaves/d	9	0.61	0.08
Estimated consumption of groundwater by crickets via greenfall ($G \times$ PC $\times$ WC)	g H_2O·m^{-2}·d^{-1}	NA	0.085	0.0019
Cottonwood transpiration#	g H_2O·m^{-2}·d^{-1}	††	6500–14 700	
San Pedro discharge ‖	g H_2O/d	1	6.9×10^9	

Note: NA indicates "not applicable" (sample sizes not reported for estimated values).

† Composite samples of 4–5 leaves per sample were collected to ensure that adequate water could be extracted. Means thus represent a larger sample size than the three leaves collected, but the SD likely does not capture the full range of variation in values for this parameter.

‡ Resting water demand is defined as resting water loss in laboratory conditions in dry air and constant temperature (see *Methods* for more detail).

§ Estimated density in two plots in distal portions of the meander bend forest at Gray Hawk.

¶ 2006 leaf addition experiment; range represents values from near and distal habitats.

Average of permanent and intermittent sites at the San Pedro (Williams et al. 2006).

‖ Average daily discharge for April–July converted to grams.

†† See Gazal et al. (2006) for information on N.

effects on regional water cycles, components of regional water cycles, even very small ones, may have pronounced effects on the performance and abundance of animal species.

In this paper, we demonstrate that wide floodplain forests provide water to terrestrial animals in deserts via subtle, indirect pathways. At our study sites at the San Pedro River in southeast Arizona, transpiration and subsequent greenfall by phreatophytic trees provides an indirect source of groundwater to animal species on the forest floor. A very common invertebrate detritivore, the damp-loving field cricket (*G. alogus*), in turn seeks water through consumption of these freshly fallen leaves (greenfall) where surface water is too far away. These crickets are one of the numerically dominant invertebrate taxa in leaf litter on the forest floor (Sabo et al. 2005) and provide a bridge between the groundwater delivered by plants to the surface and higher trophic levels (e.g., spiders, lizards, birds, mammals). Finally, we show that the magnitude of water flux via greenfall is sufficient to offset significant water loss by this animal consumer despite the seemingly trivial magnitude of the flux compared to transpiration or river discharge.

Riparian oases: gallery forests in desert river floodplains

The harsh conditions in desert environments can greatly influence the performance and constrain the distribution and abundance of animals via effects on individual energy and water budgets (Porter and Gates 1969, Noy-Meir 1974). Desert rivers and their riparian

forests present oases from these harsh conditions, where water is often plentiful (though declining in many areas of the world) and temperatures are moderated by cooler discharging groundwater. Longitudinally, the San Pedro River and other desert rivers feature two very distinct types of CWW gallery forest: ribbon gallery (~10–25 m wide in the upper watershed, and widening to 150 m on the lower river) and more expansive gallery forests in wide floodplains (ranging from 1 to 4 ha in area; Fig. 1). These floodplain gallery forests have negligible moisture in shallow soils during the dry season except immediately adjacent to the river (J. L. Sabo, *unpublished data*). Moreover, our microclimate data demonstrate that absolute humidity declines significantly within CWW gallery within 100 m from the river, and that the river modifies minimum and maximum temperature only in near-river environments. This means that gallery forests in wide floodplains provide relief for animals from some of the harsh conditions of the nearby desert (e.g., solar radiation, air temperature, scarcity of moist food) but not direct alleviation of water limitation unless very close to surface water via the river. By contrast, our results suggest that the more expansive forests in wide floodplains provide relief from water stress indirectly by the activities of phreatophytic trees. Greenfall from these trees increases the water supply and productivity of basal consumers in riparian forests, even far from surface water. As a result, wide floodplain forest habitats like those present on the upper San Pedro River represent a unique habitat type in desert habitats

where animals less equipped to survive in the nearby desert can persist, if not proliferate.

Ground water resource tracking by G. alogus in floodplain oases

Our cafeteria experiments demonstrate that *G. alogus* may compensate for higher water losses associated with drier microclimates in distal floodplain habitats by seeking water in greenfall from cottonwood trees. The experiments were designed to assess whether crickets seek greenfall primarily to obtain water, rather than other resources found in leaves of cottonwood and other tree species. Specifically, we compared percentage of attacks and consumption of wet and dry cottonwood leaves. A comparison of attacks and consumption of dry leaves (both brown and green) and wet green leaves served as a test of the effect of leaf water content on leaf consumption by *G. alogus*. These consumers attacked wet leaves more frequently and completely in distal habitats, but not in near-river habitats where surface water is more readily available. Moreover, our dry green leaf treatment served as a control for the higher C:N (lower nutrient content) of abscised leaves relative to those freshly collected from the tree. In addition to this control, we used wet leaves of two species of plants with lower C:N (higher nutrient content) to assess whether *G. alogus* chose plant resources based on N content or simply the presence of water. Finally, we conducted all trials in dry (distal) and wet (near-river) portions of a floodplain gallery forest and during dry and wet (monsoon) portions of the growing season of this animal. Our combined results suggest that *G. alogus* seek out wet cottonwood leaves in distal portions of dry floodplain forests in order to maximize their water intake and alleviate water stress.

Our evidence for this conclusion stems from three observations. First, wet cottonwood leaves are preferred to dry cottonwood leaves in floodplain gallery forests far from river water but not immediately adjacent to this source of free water. Thus, *G. alogus* avoid dry leaves, regardless of their C:N content, but still consume wet leaves when surface water is limiting. This result may arise from a preference by these detritivores for leaves with high water content, or because they cannot consume and process nutrients from dry leaves. Our observation of nonzero percentage of attacks on dry leaves (green and brown) but extremely low consumption of these leaf types suggests that dry leaves can be eaten, but are not readily consumed when wetter leaves are present. Second, preferential consumption of wet leaves in distal portions of wide floodplains occurs only during the dry season, not during the wet season, when AH is much higher across the entire floodplain and soils are saturated by rain. This result provides indirect support of the hypothesis that wet green cottonwood leaves are chosen by *G. alogus* in order to maintain positive water balance. Finally, preferential consumption of wet leaf species with low C:N (higher N content)

is stronger where surface water is more readily available (near-river vs. distal habitats) and during the wet vs. dry season, again when water is not limiting. Specifically, percentage of attacks on cottonwood leaves (lowest N content and highest water content) are equal to those of willow (highest N content and lower water content) in distal habitats during both dry seasons. By contrast, attacks on willow are consistently higher than on cottonwood and seep willow in near-river habitats during both dry seasons. Moreover, there is a trend toward higher attacks on willow in both habitats during the wet season of both years. Thus, in terms of attacks, *G. alogus* seek wet leaves in distal habitats and wet leaves with high N content in near-river habitats where water is less limiting.

These patterns are reinforced by considering the percentage consumption of each leaf type (Fig. 6). Percentage consumption of cottonwood and willow leaves are nearly equal and higher than that of seep willow during the dry season of 2005, whereas consumption of cottonwood and seep willow are nearly equal and higher than that of willow during the dry season of 2006. These patterns could be related to the observation of high herbivory and the incidence of a sticky leaf exudate on seep willow leaves during the summer of 2005 but not 2006. Alternately, leaf C:N for these tree species may vary strongly from year to year. We cannot test these two hypotheses with our current data set.

Finally, we note here that the comparison of percentage consumption of the three species of wet leaves by *G. alogus* is confounded by strong differences in the relative size of leaves of these three plant species (Fig. 7). Cottonwood leaves are larger than both willow and seep willow, and typically, seep willow leaves are slightly larger than willow leaves at our field site. Thus, total consumption of wet cottonwood leaves was always higher than that of wet willow and seep willow during the dry season (Appendix B). This is not surprising because cottonwood greenfall has typically higher water content than willow greenfall despite initially higher water content of the latter when first collected from the tree (Fig. 7). Cottonwood leaves hold water for longer periods of time, than seep willow or willow and only cottonwood leaves consistently retained some moisture through the 12-hour deployment in our experiment (J. Sabo, *personal observation*).

Comparison of greenfall flux magnitude to population water demand by G. alogus

In this paper, we provide estimates of the water demand by individual *G. alogus* based on laboratory measurements of EWL. We then scale these individual measurements to the level of the population (for representative patches of this population at our study site) using point estimates of *G. alogus* activity abundance. Our results suggest that the water supplied by greenfall is more than sufficient to offset water loss in

harsh environments experienced by *G. alogus*. Thus, the water stress recorded in field collected *G. alogus* during the day (Fig. 4), may be more than offset by foraging activities and consumption of greenfall by night.

There are a number of potential caveats that may diminish the congruence of our estimates of water demand by cricket populations and the water flux provided by greenfall. First, evaporative water loss (EWL) as we have measured it (gravimetrically in laboratory conditions) is a measure of total water efflux at rest and without food (Hadley 1994). In field conditions, these animals may experience a variety of other gains and losses of water, including those associated with consumption, excretion, and reproduction (egg laying). Moreover, evaporative losses (total water loss in the field) may be much higher when animals are active due to increased rates of respiration and associated water loss. Overall, our gravimetric measures of EWL are likely underestimates of total water demand by individual *G. alogus* at a given temperature in field conditions unless behavioral thermoregulation (refuge in dry leaf litter) and daily cycles of temperature and humidity offset increased losses due to activity. Moreover, our estimates of the water supplied by greenfall include only preformed water, and thus underestimate total water acquisition by crickets via greenfall by ignoring water produced by catabolism of the organic leaf material. However, in most situations, water produced during catabolism is a relatively small source (Hadley 1994). Despite these potential complications, the estimated flux of water via greenfall is ~2.5 times higher than EWL at rest in an environment of 0% AH and constant 30°C, which suggests that the water supply is potentially adequate to sustain observed high densities of *G. alogus* even when we account for activity and other field complexities.

A second potential caveat is that there are other invertebrates that need water and that could acquire this water via greenfall. Though field crickets are the primary consumer of greenfall in our system, small mammals and other invertebrate detritivores (e.g., camel crickets, cockroaches, and isopods) are all capable of eating greenfall to some degree.

Finally, the abundance of *G. alogus* is spatially variable and appears to be strongly dependent on litter cover and local microclimate (J. Sabo and K. McCluney, *personal observation*). Here, we only measured activity abundance in four cleared plots. We did this because it is straightforward to count crickets in cleared plots, and litter-free habitat is preferred by crickets at night (J. L. Sabo, *unpublished data*). Activity abundance is likely a good estimate of density in cleared plots, but cleared plots are not necessarily representative of forest floor environments at our study site. Representative density estimates likely range from 0.5 to 2 (or more) crickets/m^2. Thus our estimates are on the low end, potentially underestimating population-level water demand by *G. alogus*.

Given these three potential caveats our conclusion that greenfall is sufficient to support cricket populations in the absence of surface water may be weakened, though not significantly. For example, if we assume true estimates of cricket density to be fourfold higher than measured here and an equivalent density of other invertebrate consumers of greenfall our total demand for water from greenfall would be eightfold higher than in Table 4. Assuming that increases in EWL associated with respiration, activity, and excretion are offset by inactivity and refuge in cooler, moister microenvironments (e.g., under leaf litter) during peak heat in the day (e.g., use 30°C lab data), we arrive at a community demand for greenfall water of ~0.316 g·m^{-2}·d^{-1}. When compared to the flux of water from greenfall (~0.14 g·m^{-2}·d^{-1}) this would suggest that greenfall can provide nearly 45% of the total water budget for these animals even when considering very liberal (high) estimates of the true density of crickets and other greenfall consumers on the forest floor.

These caveats are likely the most conservative set of circumstances such that groundwater provides the majority, if not all water to *G. allogus* during the dry season at our study sites. The observation that not all attacked greenfall is consumed on a daily basis (Table 4; Fig. 6) combined with negligible soil moisture and sparse herbaceous vegetation at our study sites supports the idea that the water delivered by greenfall likely exceeds the daily demand of forest floor invertebrates in our system. Thus, we suspect that our conclusion that greenfall can sustain the entire population of *G. alogus* on wide floodplains is robust even under these conservative circumstances. Nevertheless, a broader test of these ideas across a larger sample size of similar floodplain gallery forest on the San Pedro River is warranted before we can generalize these results to similar desert river systems.

Conclusion

Our results have several implications for both basic ecology and the management of riparian ecosystems in arid lands. First, connectivity between subsurface and surface ecosystems demonstrate that this boundary is one of convenience (Wardle 2002): plants connect below ground pools of materials to above ground consumers and their food webs. In this case, we have demonstrated novel links between below ground hydrology and the foraging decisions and abundance of an aboveground animal species.

Second, phreatophytes in floodplain gallery forests increase the total water supply available to surface consumers in floodplain ecosystems. Wide floodplain forests along desert rivers may be more valuable to animal species than the narrow ribbons of forest, characteristic of degraded (incised) river channels. Large gallery forests in wide floodplains supply more water to above ground consumers by virtue of their sheer area and thus, potentially increase the spatial extent of tolerable

conditions for primary consumers in desert floodplains. These primary consumers in turn provide a conduit for groundwater between plants and higher trophic levels. For example, consumption of crickets by predatory spiders (*Hogna anteleucana*) is significantly reduced by experimental additions of free (drinking) water (K. E. McCluney and J. L. Sabo, *unpublished manuscript*), suggesting that these predators augment consumption of crickets to meet high water demands when free water is unavailable. More broadly, the San Pedro River hosts over 350 species of breeding and migratory birds and as many as 4 million individuals use the river as a migratory corridor (The Nature Conservancy 2008). Though consumption of direct surface water is likely important, it is not always available (in dry reaches or dry years). In these situations, high abundance of animals at higher trophic levels may be sustained by groundwater via the herbivores and detritivores that consume cottonwood leaves or photosynthate. Wide floodplain forests likely direct more groundwater to these migratory species by fueling higher abundances of primary consumers in the canopy and on the forest floor.

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APPENDIX A

Methods and calculations associated with comparing water supply (via greenfall) and population demand by crickets at the scale of the floodplain (Ecological Archives M078-025-A1).

APPENDIX B

Estimated total consumption of leaves in the cafeteria experiment (Ecological Archives M078-025-A2).