Spatial and Temporal Patterns in Insectivorous Bat Activity in River-Riparian Landscapes

By

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ABSTRACT

River and riparian areas are important foraging habitat for insectivorous bats. Numerous studies have shown that aquatic insects provide an important trophic resource to terrestrial consumers, including bats, and are key in regulating population size and species interactions in terrestrial food webs. Yet these studies have generally ignored how structural characteristics of the riverine landscape influence trophic resource availability or how terrestrial consumers respond to ensuing spatial and temporal patterns of trophic resources. Moreover, few studies have examined linkages between a stream's hydrologic regime and the timing and magnitude of aquatic insect availability.

The main objective of my dissertation is to understand the causes of bat distributions in space and time. Specifically, I examine how trophic resource availability, structural components of riverine landscapes (channel confinement and riparian vegetation structure), and hydrologic regimes (flow permanence and timing of floods) mediate spatial and temporal patterns in bat activity. First, I show that river channel confinement determines bat activity along a river's longitudinal axis (directly above the river), while trophic resources appear to have stronger effects across a river's lateral (with distance from the river) axis. Second, I show that flow intermittency affects bat foraging activity indirectly via its effects on trophic resource availability. Seasonal river drying appears to have complex effects on bat foraging activity, initially causing imperfect tracking by consumers of localized concentrations of resources but later resulting in disappearance of both insects and bats after complete river drying. Third, I show that resource tracking by bats varies among streams with contrasting patterns of trophic resource availability and this variation appears to be in response to differences in the timing of aquatic insect emergence, duration and magnitude of emergence, and adult body size of emergent aquatic insects. Finally, I show that aquatic insects directly influence bat activity along a desert stream and that riparian vegetation composition affects bat activity, but only indirectly, via effects on aquatic insect availability. Overall, my results show river channel confinement, riparian vegetation structure, flow permanence, and the timing of floods influence spatial and temporal patterns in bat distributions; but these effects are indirect by influencing the ability of bats to track trophic resources in space and time.

DEDICATION

I dedicate this dissertation to my daughter, Emma Rose Hagen Beversdorf.

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CHAPTER 1

INTRODUCTION

Aquatic and terrestrial ecosystems are connected by flow of energy, material, and organisms (hereafter, ‘resources’) that link production in one habitat to consumers in an adjacent habitat (Hynes 1975). Traditionally, resource flow in watershed ecosystems has been best understood via the ubiquitous, gravity-fed flows of terrestrially derived resources (e.g., leaves) to aquatic systems (Fisher and Likens 1973, Wallace et al. 1997). This traditional view of food webs is changing though, and the reciprocal exchange of resources across aquatic-terrestrial boundaries (Nakano and Murakami 2001) is now the more accepted paradigm (Baxter et al. 2005). The reciprocal flow of resources from the water to the land can have large effects on terrestrial community structure (Polis and Hurd 1996). Empirical evidence documenting the magnitude of resource flow (Jackson and Fisher 1986) and its effect on the abundance, distribution, and behavior of organisms in the recipient ecosystem are plentiful (Polis and Hurd 1996, Nakano et al. 1999a, Sabo and Power 2002b). Nevertheless, few studies have focused on how characteristics of the riverine landscape mediate the magnitude of resource flows or the active movement of animals (Marczak et al. 2007), or how consumers, in turn, respond to ensuing spatial and temporal patterns of resource availability (Nakano and Murakami 2001, Stapp and Polis 2003). Moreover, few studies have attempted to link a river’s hydrologic regime to the timing and magnitude of resource supply from aquatic donor to terrestrial recipient ecosystems. The main objective of my dissertation research is to understand the causes of terrestrial consumer distribution patterns in space and time. Numerous studies have examined how individuals track spatially variable resource patches (MacArthur and Pianka 1966, Zollner and Lima 1999) or how individuals respond to temporally pulsed resources (Ostfeld and Keesing 2000). However, these studies have primarily occurred within one ecosystem and have not examined how individuals respond to spatial and temporal variability in resources generated in donor ecosystems. In this dissertation, I examine how contrasting patterns of insect resource availability, structural components of the riverine landscape, and hydrologic regimes mediate temporal and spatial variability in terrestrial consumer abundance and hence, the magnitude of aquatic-terrestrial linkages.

Aquatic insects provide an important food resource to terrestrial consumers, making up 25-100% of the energy supply to riparian consumer diet (reviewed by Baxter et al. 2005). The contribution of aquatic insects to terrestrial consumers can be quite large along desert streams. For example, aquatic insects supplied almost 100% of spider energy requirements along Sycamore Creek, a Sonoran Desert stream, during a 6-week period in May-June 1997 (Sanzone et al. 2003). While numerous studies have shown that aquatic insects provide an important food resource to terrestrial consumers, these studies generally have been short in duration and do not consider temporal or spatial variability in aquatic insect availability (Kawaguchi and Nakano 2001, Nakano and Murakami 2001). Aquatic insect emergence is temporally variable (Corbet 1964, Kawaguchi and Nakano 2001). Peak emergence is generally highest during early summer months and declines by late summer in temperate streams (Sweeney and Vannote

1982), whereas rates of aquatic insect emergence can be fairly constant throughout the summer in desert streams (Jackson and Fisher 1986). The timing of aquatic insect emergence is also closely tied to the hydrologic regime (Whiles et al. 1999). For example, peak aquatic insect emergence from desert streams generally occurs prior to the late-summer monsoon season (Lytle 2002). Availability of aquatic insects varies spatially as well. Spatial variation in aquatic insect emergence is related to stream habitat type (riffle versus pool), algal productivity, and detritus availability (Iwata 2007).

While peak rates of insect emergence may be highly variable, even low quantities of emergent aquatic insects can provide an energy resource to terrestrial consumers throughout most of the year (Jackson and Fisher 1986, Nakano and Murakami 2001). Terrestrial consumers may compensate for variable aquatic insect availability through behavioral changes. Nakano and Murakami (2001) found that aquatic insects made up the largest proportion of bird diet (50-90%) November through May, which coincided with senescence of riparian tree foliage and reductions in terrestrial insect availability. However, during leaf-out periods, when terrestrial insect availability was high and aquatic insect availability low, birds switched their foraging efforts to terrestrial insects. Bat foraging activity is highest from spring to early fall (O'Farrell and Bradley 1970, Kuenzi and Morrison 2003). Bats may compensate for changes in aquatic insect availability by switching to another food source, entering extended periods of torpor, hibernating or migrating during times of year when insects are less available.

Temporal and spatial variability in aquatic insect availability may be an important factor influencing the overall effect of aquatic resources on terrestrial consumers.

My dissertation research focuses on insectivorous bats, an abundant and speciose group of terrestrial consumers in stream-riparian ecosystems. Bats are highly mobile consumers and are better able to sample and compare widely spaced habitats than less-mobile taxa with less 'ideal' (*sensu* Fretwell and Lucas 1970) knowledge of the lay of the land. Several studies have shown the importance of streams and riparian areas as foraging habitat for insectivorous bats (Rydell et al. 1994, Walsh and Harris 1996, Grindal et al. 1999, Warren et al. 2000, Seidman and Zabel 2001, Law and Chidel 2002, Russo and Jones 2003). Previous studies show intensive foraging activity directly over stream channels and riparian areas, but little activity beneath or within dense forest canopies (Thomas 1988, Power et al. 2004). This is often attributed to high aggregations of emergent aquatic insects, which provide an important food resource to foraging bats (Belwood and Fenton 1976, Racey and Swift 1985, Brigham and Fenton 1991, Brigham et al. 1992, Fukui et al. 2006). Structural features of the riverine landscape may also influence bat foraging activity. For example, riparian vegetation provides protection from wind and rain (Verboom and Spoelstra 1999), as well as predators (Rydell et al. 1996). Moreover, ambient light is reduced under riparian vegetation, providing bats protection from diurnal avian predators earlier in the evening than in open habitats with no overhead vegetation (Rydell et al. 1996). In contrast to these positive effects of riparian vegetation, plants may also limit bats' ability to maneuver during flight and constrain echolocation ability (Ober and Hayes 2008a). Similarly, river channel geomorphology may also constrain flight paths and concentrate bats (i.e., in narrow channels). Previous studies have shown that the abundance of riparian birds was strongly related to characteristics of the stream channel such as sinuosity (Iwata et al. 2003). In addition to structural characteristics of riverine landscapes, hydrologic conditions likely affect aquatic-terrestrial linkages. Numerous studies have examined how benthic aquatic insects respond to flood disturbances (Fisher et al. 1982, Grimm and Fisher 1989, Boulton et al. 1992, Lytle and Poff 2004, Boulton et al. 2006) and reductions in surface water flow (e.g., Lake 2003, Dewson et al. 2007). However, the response of terrestrial consumers to hydrologic conditions has largely been ignored. Hydrologic conditions likely have strong effects on insectivorous bats that depend on surface flows for trophic resources and drinking water.

To examine how trophic resource availability, structural components of the riverine landscape, and hydrologic conditions influence spatial and temporal variability in insectivorous bat activity in riverine landscapes, I conducted 4 studies that are presented in the following 4 chapters. In Chapter 2, I examined how trophic resource availability, river channel geomorphology, and riparian vegetation physiognomy influenced spatial patterns in bat activity. This study was conducted along the **South Fork Eel River**, California. The **South Fork Eel River** is a highly productive river characterized by warm, dry summers and mild, wet winters. This river alternates between sections of canyons (confined reaches) and open floodplains (unconfined reaches). Rock bars with cobble to boulder-size substrate lay adjacent to the river along unconfined reaches. Some of the rock bars were lined with a narrow band of riparian vegetation (*Alnus glutinosa*) along the river edge, while others were not. These contrasting reach types allowed me to examine how insect availability, channel confinement, and riparian vegetation influenced spatial patterns in bat activity both above the river and in the floodplain. In this study, channel confinement, not aquatic insect availability, determined the location of bat activity along a river's longitudinal axis, while aquatic insects appeared to have strong effects on the location of bat activity across the river's lateral transect.

The **South Fork Eel River** was an ideal system to examine relationships between river channel geomorphology and the location of bat foraging activity due to strong contrasts in channel confinement. However, the **South Fork Eel River** did not exhibit much hydrologic variation. Desert streams, on the other hand, exhibit strong variation in the magnitude, timing, and duration of flow conditions. Thus, examining the relationship between hydrologic conditions and bat activity was deemed more suitable along desert streams. Thus, the remainder of my dissertation research was conducted in desert stream ecosystems.

In Chapter 3, I examined the effects of trophic resource availability, flow permanence, and river drying on temporal patterns in bat activity. This study was conducted along the **San Pedro River**. The **San Pedro River** flows north from Sonora, Mexico into southeastern Arizona and is one of the last entirely free-flowing rivers in the desert Southwest. The **San Pedro River** valley is recognized internationally for its high biological diversity, which includes thousands of species of microorganisms and insects, over 55 species of reptiles and amphibians (Rosen 2009), more than 400 species of birds (Krueper 1999), and over 80 species of mammals (Soykan et al. 2009), including 24 species of bats (Hanson 2001), making up more than half of the species of bats found in the United States and Canada (Nowak 1994). In addition to high bat diversity, the **San Pedro River** valley is a rare remnant of the Fremont cottonwood-Goodding willow (*Populus fremontii* and *Salix gooddingii*) gallery forest type, which is declining in many places throughout the arid Southwest in response to extensive groundwater declines (Stromberg 2007), but increasing in a few rivers including the upper San Pedro River watershed (Webb and Leake 2006, Stromberg et al. 2010). While the San Pedro River still maintains perennial flows in much of its upper watershed, regional drought, groundwater declines, as well as localized groundwater pumping have resulted in transitions from perennial to interment and ephemeral flow along sections of the river (Leenhouts et al. 2006). Further, groundwater pumping is contributing to the increased frequency of river drying (Stromberg et al. 2006). In this chapter, I measured bat activity and insect availability at perennial and intermittent sites. Bats seemed to track declines in aquatic insect availability throughout the summer dry season, but only at perennial sites. I also examined the consequences of river drying on bat activity and insect availability. As the river dried, aquatic insects and bats nearly disappeared, despite increases in terrestrial insect abundance and biomass. Intermittency and river drying seems to have complex effects on bat activity, initially causing imperfect tracking of food resource, followed by disappearance of both aquatic insects and bats after the river dries completely.

In chapter 4, I present results from a year-long study where I examined how trophic resource availability and hydrologic regime influenced spatial and temporal patterns in bat activity. This study was conducted along 2 Sonoran Desert streams that exhibit contrasting hydrologic regimes, riparian vegetation structure, and aquatic primary productivity, which contribute to different patterns of insect availability: **Sycamore Creek** and the **San Pedro River**. **Sycamore Creek** is characterized by a winter flood-regime and a narrow band of riparian trees, while the **San Pedro River** has a monsoon flood-regime and supports an extensive closed canopy gallery forest. **Sycamore Creek** is an intermittent stream characterized by high primary productivity, secondary productivity, and aquatic insect emergence rates (Jackson and Fisher 1986, Mulholland et al. 2001). Less is known about emergence at the **San Pedro River**, but previous work suggested that emergence occurs prior to the summer monsoon (E. M. Hagen, personal observation). Results of this study suggest that temporal and spatial patterns in insect availability vary widely among desert streams. Further, tracking of insect prey by bats varied between the 2 study sites and this variation appeared to be due to differences in aquatic insect availability. Strong positive relationships between bats and aquatic insects at Sycamore Creek may be related to high aquatic productivity, strong asynchrony in aquatic and terrestrial prey availability, and limited riparian habitat. Nearly equal proportions of aquatic and terrestrial insects and extensive and diverse riparian habitats along the river can explain weak or non-significant relationships between bats and aquatic insects but strong relationships between bats and total insects at the San Pedro River.

In Chapter 5, I present the results of a large-scale experimental reduction of aquatic insect emergence from 2 reaches of the **San Pedro River** with contrasting riparian vegetation structure. Specifically, I compared bat activity along a reach with high structural complexity, which was characterized by cottonwood, willow, and tamarisk vegetation, to a reach with low structural complexity that consisted of tamarisk vegetation but no cottonwood or willow vegetation. Two 50-m exclosures set in reaches with contrasting riparian vegetation structure allowed me to examine how structural characteristics of riparian vegetation and food resource availability influenced bat distributions within a desert-riverine landscape. Exclosures significantly reduced aquatic insect availability and bat activity above the river in both types of riparian vegetation structure. I also found significantly higher aquatic insect abundance and bat activity along the reach with high structural complexity, suggesting that aquatic insect availability rather than structural complexity influenced the location of bat activity along the **San Pedro River**.

Finally, I include the results of 2 side projects I've undertaken while at Arizona State University. Appendix A consists of a book chapter that characterizes the flow of detritus across aquatic-terrestrial boundaries and examines the effects of detritus on recipient populations, communities, and ecosystems. This book chapter stems from participation in a National Center of Ecological Synthesis (NCEAS) Working Group titled Dynamic Deserts. This chapter will be published in *Detritus and the Dynamics of Populations, Food Webs and Ecosystems,* edited by J. C. Moore, M. Vanni, P. de Ruiter, A. Hastings, and A. Rosemond.

Finally, Appendix B contains the results from a meta-analysis conducted by the Sabo Lab in which we examined the effects of detritus on primary producers and consumers in a wide variety of ecosystem types. Specifically, we asked four questions about how detritus affects food web structure in a wide variety of ecosystems: 1) what is the effect strength of detritus on primary producers, detritivores, herbivores, and predators?, 2) what functional role does detritus serve for consumers (energetic, habitat, or both)?, 3) how does the effect of detritus on consumers vary between aquatic and terrestrial ecosystems?, and 4) does detritus catalyze top-down control of predators on living plant tissue? This study suggests that detritus has strong positive effects on primary producers and consumers in a wide range of ecosystem types. Detritus has a positive effect on detritivores by providing an energetic resource and both energetic and habitat resources. Detritus also has an equally strong and positive effect on herbivores and predators by providing a habitat resource. Detritus has strong positive effects in both aquatic and terrestrial ecosystems, with stronger effects in terrestrial ecosystems. Finally, results of this study suggest that detritus has bottom-up effects via fertilization of primary producers.

CHAPTER 2

A LANDSCAPE PERSPECTIVE ON BAT FORAGING ECOLOGY ALONG RIVERS: DOES CHANNEL CONFINEMENT AND INSECT AVAILABILITY INFLUENCE THE RESPONSE OF BATS TO AQUATIC RESOURCES IN RIVERINE LANDSCAPES?

Abstract. River and riparian areas provide important foraging habitat for insectivorous bats owing to high insect availability along waterways. However, structural characteristics of the riverine landscape may also influence the location of foraging bats. I used Anabat II bat detectors to compare bat activity longitudinally along river reaches with contrasting channel confinement and riparian vegetation, and laterally with distance from the river along 3 different reach types. I measured rates of insect emergence from the river, and aerial insect availability above the river and laterally up to 50-m into the riparian habitat, to assess the relationship between trophic resources and insectivorous bats. Longitudinally, bat activity was concentrated along confined reaches in comparison to unconfined reaches but was not related to insect availability. Laterally, bats tracked exponential declines in aquatic insect availability with distance from the river. These data suggest that along the lateral dimension bats track trophic resources, but that along the longitudinal dimension channel shape and landscape structure determine bat distributions more than trophic resources.

INTRODUCTION

Several studies have shown that rivers and riparian areas provide important foraging habitat for insectivorous bats (Walsh and Harris 1996, Seidman and Zabel 2001, Law and Chidel 2002, Russo and Jones 2003). These studies suggest that bat activity, density, and distribution are related to trophic resource availability in these habitats. Aquatic insects make up a large portion of insectivorous bat diet (Belwood and Fenton 1976, Racey and Swift 1985, Sullivan et al. 1993, Racey 1998). Higher rates of foraging activity within river and riparian habitat in comparison to upland habitats are often attributed to higher aquatic insect availability along waterways (Racey and Swift 1985, Brigham and Fenton 1991). Further, the experimental reduction of aquatic insect availability has been shown to reduce bat foraging activity (Fukui et al. 2006).

Structural characteristics of riverine landscapes (channel geomorphology and riparian vegetation physiognomy) may also influence insectivorous bat distributions. For example, rivers provide more open airspace for navigation and foraging in comparison to more cluttered terrestrial habitats. In an Oregon Coastal Range forest, riparian vegetation concentrated insectivorous bat activity directly over the stream channel (Ober and Hayes 2008a). Riparian vegetation seemed to restrict bat activity by hindering flight maneuverability and echolocation. Rivers effectively create gaps in dense forest vegetation that allow for unobstructed flight and foraging by echolocating bats. As a result, a few studies have shown intensive foraging activity directly over river channels, but little activity beneath or within dense forest canopies (Thomas 1988, Power et al. 2004). In contrast to this work on trophic determinants of bat foraging activity, there have been fewer studies assessing the role of riverine landscape structure in determining bat activity. Here, I examine how two types of riverine landscape structure, river channel confinement and riparian vegetation physiognomy, may affect the location of bat foraging activity. Specifically, my goal is to examine how strongly trophic (food resource availability) and structural characteristics of the landscape (channel confinement and riparian vegetation physiognomy) influence bat activity and density. I examine the effect of trophic resources and riverine landscape structure along both longitudinal (directly above the river) and lateral (with distance from the river) dimensions. These two dimensions were selected as both longitudinal and lateral dimensions are expected to influence the exchange of organisms between aquatic and terrestrial ecosystems. Further, combining ecological and geomorphological perspectives will provide a more comprehensive understanding of factors influencing ecosystem structure and function (Poole 2002).

Trophic resources vary both longitudinally among different reach types and laterally with distance from the river. Longitudinal variation in aquatic insects availability may be related to riverine productivity. For example, strongly confined river reaches generally receive fewer hours of sunlight leading to lower primary and secondary production in comparison to unconfined river reaches (Stanford and Ward 1988, Ward and Tockner 2001). Extensive riparian vegetation may also reduce light penetration to the river limiting river productivity (Cummins et al. 1989, Tait et al. 1994, Boothroyd et al. 2004). Thus, aquatic insect availability is expected to be lower along confined reaches and unconfined reaches with riparian vegetation than unconfined reaches without riparian vegetation. Exponential declines in aquatic insect abundance and biomass with lateral distance from the river have also been documented along several rivers (e.g., Iwata et al. 2003, Power et al. 2004). River channel geomorphology has been shown to influence lateral movement of insects between aquatic and terrestrial ecosystems (Malmqvist 2002). Specifically, river channel topography influences the lateral dispersal of aquatic insects into the terrestrial landscape (Iwata et al. 2003).

Longitudinal and lateral variation in trophic resources and riverine landscape structure will likely influence terrestrial consumer activity, density, and distribution. For example, Iwata et al. (2003) found that the abundance of riparian birds (fly catchers and gleaners) was strongly related to characteristics of the stream channel (sinuosity). Elevated bird abundance along highly meandering streams was likely in response to higher aquatic insect abundance resulting from longer stream edge habitat and surface area (Iwata et al. 2003). River confinement may have a similar effect on bat activity such that steep topography along confined river reaches may effectively increase the density of aquatic insects directly above the river, while unconfined reaches may promote the lateral dispersal of aquatic insects into the terrestrial landscape. Nevertheless, the effects of landscape structure have largely been ignored when describing bat activity, density, and distributions.

The purpose of this study was to examine the relative importance of riverine landscape structure and trophic resources on bat activity and density along both longitudinal and lateral dimensions. Here the longitudinal dimension is defined as a ~5-km reach of river over which channel confinement and riparian forest physiognomy are spatially variable. The lateral dimension is the valley cross section in a river segment (from river's edge to 50 m from the river), across which elevation varies as a result of channel shape (or 'confinement') and the variable presence of riparian trees. I chose these measures of landscape structure because previous research and observations have shown that riparian consumers (including bats) respond to spatial and temporal variation in insect availability along both of these dimensions (Power et al. 2004). I asked how channel confinement, riparian vegetation physiognomy, and food resources influence bat activity and density along both longitudinal and lateral dimensions.

METHODS

Study Site

This study was conducted along a ~5-km reach of the South Fork Eel River (39° 44' N, 123° 39' W) in Mendocino County, California, USA, May – August 2006 (Fig. 1). Mendocino County's climate is Mediterranean consisting of rainy winters followed by summer droughts; most of the annual rainfall occurs October through May. During this study, mean air temperature above the river channel was 18°C. The South Fork Eel is a highly productive river and most reaches of the river receive 6-8 hours of sunlight per day. Summer base flow ranges from 2 – 4.5 $m^3 s^{-1}$ and peak flood discharge during heavy winter storms can reach 56 $m^3 s^{-1}$ (Power et al. 2004). Heavy winter floods have scoured the active river channel, so that in places, the valley floor is much wider than the river during summer base flow. The river is characterized by alternating sections of canyons (confined reaches) and open floodplains (unconfined reaches).

Unconfined reaches were adjacent to rock bars with cobble to boulder size substrate. Rock bars ranged between 25 – 70 m wide and were bordered by the river on one side and forest or grassy meadow on the other. Some of the rock bars exhibited alder (*Alnus glutinosa*) encroachment directly adjacent to the river. Upland habitats consisted of mixed coniferous-deciduous forest dominated by Douglas fir (*Pseudotsuga menziesii*) and oak species (*Quercus* spp.) and grassy meadows (Sabo and Power 2002b).

Five species of bats were identified via mist netting along the South Fork Eel River: *Myotis yumanensis*, *M. californicus*, *M. thysanodes*, *M. lucifugus*, and *Eptesicus fuscus* (Appendix C: Table 21). These species generally roost in high elevations in forested watersheds in cavities of trees, caves, mines, and rock outcrops (Pierson 1998) but forage directly above the river (Power et al. 2004). Specifically, these species tend to forage over slow-flowing water and pools (Herd and Fenton 1983, Brigham et al. 1992). Most of these species are aerial hunters capturing insects during flight; however, some glean insects from the surface of water (e.g., *M. yumanensis*, *M. lucifugus*) or vegetation (e.g., *M. californicus*). It is unknown how riverine landscape structure may influence critical foraging habitat for these species.

To assess how structural features of the riverine landscape influence bat activity, I selected sites along river reaches that were characterized as confined, unconfined with alder vegetation, and unconfined without alder vegetation (Fig. 1). Study sites consisted of ~100-m longitudinal sections of river by 50-m lateral distance from the river. Sites were selected using digital elevation maps (DEM) created with light detection and range (LIDAR) data with bare earth, river, and vegetation layers of the South Fork Eel River watershed (Sapp and Bode 2005). Further, I measured the valley floor width and active channel width at each study site. Confinement was measured as the ratio of valley floor width to active channel width. Reaches with valley floor width to active channel width equal to or less than 2 were considered confined, while sites with valley floor width to active channel widths greater than 2 were considered unconfined (Bisson et al. 2007). Alder-stand canopy width adjacent to the river was measured at each unconfined with alder site. I selected 9 main sites along the South Fork Eel River, 3 within each site type (confined, unconfined with alder, and unconfined without alder; Fig. 1). Confined sites with alder riparian vegetation were not present preventing a 2X2 study design. Bat activity and insect availability were measured at each of the 9 main sites. Percentage canopy cover was estimated from the center of river at each main site using a densiometer. Bat activity was measured at an additional 12 sites with varying channel confinement (Fig. 1).

Active channel width ranged from 5 m at an unconfined site without alder to 35.1 m at a confined site, with no pattern among site type (Table 1). Valley floor width ranged from 18.4 m at a confined site to 80.6 m at an unconfined site with alder. Channel confinement ranged from 1.2 m at a confined site to 8.9 m at an unconfined site without alder. Alder stand width along unconfined sites with alder varied between 4.7 and 10.9 m. Canopy cover ranged from 13.9 % at an unconfined site without alder to 65.5 % at an unconfined site with alder (Table 1).

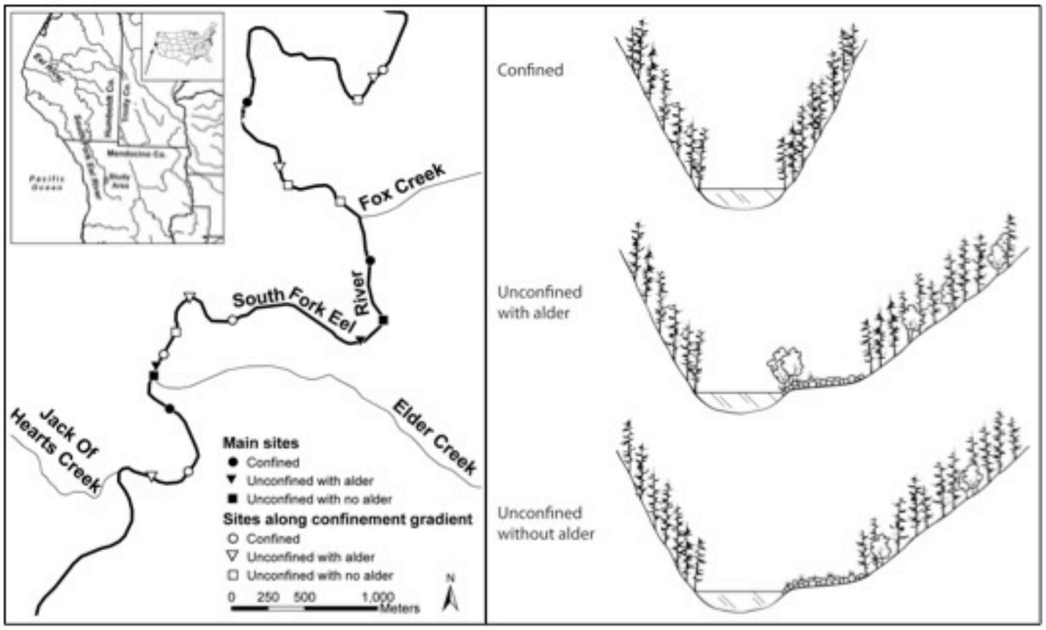

FIG. 1. Map showing study site locations and schematic showing site types along the South Fork Eel River.

TABLE 1. Characteristics of each study site.

Site type	Site name	Channel width (m)	Valley floor width (m)	Confinement	Alder canopy width (m)	Canopy cover (%)
Main sites						
Confined	Elder	12.4 (1.4)	24.2 (0.4)	2.0 (0.2)		46.4 (2.1)
Confined	Globbi	19.0 (1.0)	23.7 (0.3)	1.3 (0.1)		37.6 (3.2)
Confined	Janes	10.2 (1.3)	18.4 (1.3)	1.8 (0.2)		41.0 (1.4)
Unconfined with alder	Elder	8.6 (0.5)	37.5 (0.7)	4.4 (0.3)	10.9 (1.6)	53.4 (8.4)
Unconfined with alder	Globbi	12.6 (1.6)	63.8 (2.2)	5.2 (0.8)	7.1 (0.4)	21.3 (4.7)
Unconfined with alder	Janes	10.6 (0.8)	80.6 (5.5)	7.7 (0.8)	4.7 (0.6)	65.5 (11.9)
Unconfined without alder	Elder	11.7 (0.3)	42.6 (0.9)	3.6 (0.0)		38.1 (4.8)
Unconfined without alder	Globbi	14.4 (2.2)	69.4 (0.6)	5.0 (0.7)		13.9 (0.5)
Unconfined without alder	Janes	7.8 (0.2)	35.1 (0.9)	4.5 (0.2)		45.6 (3.3)
Sites along confinement gradient						
Confined	Walker Meadow	18.0	34.5	1.9		
Confined	White House	18.7	22.0	1.2		
Confined	Wilderness Lodge Rock Bar	35.1	42.0	1.2		
Unconfined with alder	Rattlesnake	9.6	73.0	7.6		
Unconfined with alder	Skunk	18.5	66.0	3.6		
Unconfined with alder	Walker Meadow	12.0	43.0	3.6		
Unconfined with alder	White House	17.5	44.5	2.5		
Unconfined without alder	Angelo	12.5	41.0	3.3		
Unconfined without alder	Merganser	14.2	53.6	3.8		
Unconfined without alder	Pete's Rock Bar	17.0	58.0	3.4		
Unconfined without alder	Skunk	14.5	34.5	2.4		
Unconfined without alder	White House	5.0	44.5	8.9		

Notes: Bat activity and insect availability were measured at main sites and only bat activity was measured at sites along confinement gradient. Confinement is the ratio of valley floor width to channel width. Alder canopy width is the mean width of alder canopy adjacent to the river at unconfined sites with alder. Canopy cover was measured from the center of the river channel at each main site. Values shown are means (± SE).

Longitudinal and lateral dimensions

To examine the effects of riverine landscape structure and trophic resource availability on bat activity along both longitudinal and lateral dimensions, I divide the methods of this paper into the following categories: 1) *Longitudinal bat activity* and 2) *Lateral bat activity*.

Longitudinal bat activity—We passively monitored bat activity using Anabat II bat detectors connected to zero-crossings analysis interface modules (Anabat CF Storage ZCAIM; Titley Electronics, Ballina Australia). Bat activity was measured as minutes of bat activity per night (referred to as bat activity) and minutes of bat activity per m^2 open airspace per night (referred to as bat density). Bat detectors were deployed at the 9 main sites from sunrise to sunset for 22 – 30 nights at each site between 20 May and 4 August 2006. Additionally, bat detectors were deployed for 3 consecutive nights directly above the river at all 21 sites (9 main and 12 additional) with varying channel confinement from 8 – 29 July 2006.

To control for the effects of environmental clutter (Brigham et al. 1997), bat detectors were set so that physical structure (e.g., vegetation) did not block the microphones. Detectors were deployed in plastic containers to protect from weather and microphones were oriented at 45° upwards (O'Farrell 1998). Bat detector microphones were calibrated and detected bat acoustic activity up to 9.14 m from the detector. Calls were analyzed using Analook Bat Call Analysis System (Version 4.9g) software. Analook has built in filters that search the data in each call file for smoothly connected dots. Smoothly connected dots have a high likelihood of being produced by echolocating bats. Call files were viewed using default settings for all filter parameters except for the "smooth" and "minDur" parameters. The smooth parameter was set at 15 to differentiate series of smoothly connected dots from dots separated from adjacent dots. Dots separated from adjacent dots likely resulted from wind noise. The minDur parameter was set to 1-ms so that only calls with a minimum duration of at least 1 ms were included in analysis.

Rates of aquatic insect emergence were measured using 0.25-m^2 floating emergence traps to assess trophic resource availability. Replicate (3) emergence traps were deployed for 5 days at the 9 main sites during 4 sampling periods throughout the summer. Emergence traps were deployed 19 – 31 May, 5 – 12 July, 12 – 17 July, and 1 – 8 August. After 5 days, insects collected in emergence traps were preserved in ethanol until processed in the lab.

We measured abundance of aerial aquatic and terrestrial insects at each site using sticky traps attached to rebar in the active river channel. Replicate (3) sticky traps were deployed for 5 days at the 9 main sites during 3 sampling periods throughout the summer (19 – 31 May, 5 – 12 July, and 1 – 8 August). Sticky traps consisted of projector sheets (603.2 cm^2) coated with Tangle-Trap adhesive (Tanglefoot, Grand Rapids, Michigan, USA). After 5 days, sticky traps were covered with cellophane and frozen until insects were processed in the lab.

Insects were subsampled, identified to order, except for Diptera and Coleoptera, which were identified to family using Borror et al. (1989) and Merritt et al. (2008). Insect orders and Diptera and Coleoptera families were categorized as aquatic or terrestrial. Insects were considered terrestrial only if they were the product of terrestrial secondary production (i.e., flying adult aquatic insects were categorized as aquatic insects). Aquatic and terrestrial insect abundance was determined, length was measured (±1 mm) using a Leica S6D dissecting microscope, and biomass was calculated from length-mass regressions (Sabo et al. 2002).

Lateral bat activity—To examine how river landscape structure and trophic resource availability affect bat activity laterally, I deployed bat detectors for 3 consecutive nights at 4 distances from the river (0-, 10-, 25-, and 50-m) at one site in each site type along a ~700-m reach of river. Lateral bat activity was measured in July to coincide with peak aquatic insect emergence. Bat detectors were calibrated and calls were analyzed as described in the longitudinal bat activity section above.

To measure insect availability with lateral distance from the river, sticky traps were hung ~1 m above the ground at each of the 9 main sites. At each site I established 3 replicate transects of sticky traps with lateral distance from the river. Sites were established 0-m (directly above the river), 1-, 2-, 3-, 5-, 10-, 25-, and 50-m from the river edge. Sticky traps were deployed for 5 days during 3 sampling periods (19 – 31 May, 5 – 12 July, and 1 – 8 August). Insects collected on sticky traps were processed and analyzed as described above.

Statistical analysis

Longitudinal statistical analysis—Regression analyses (simple linear regression and forward stepwise multiple regression) were used to explore relationships among bat activity, bat density, channel confinement, and aquatic and terrestrial insect abundance and biomass along the longitudinal dimension. The effects of site type and sampling period on bat activity, bat density, rates of aquatic insect emergence, and aquatic and terrestrial aerial insect abundance and biomass over time were examined using 7 separate repeated measures analysis of variances (RM ANOVA). For each analysis, the response variables were bat activity, bat density, emergence rate, aquatic aerial insect abundance, terrestrial aerial insect abundance, aquatic aerial insect biomass, or terrestrial aerial insect biomass. The explanatory variables were site type and sampling period for all RM ANOVAs. Data were transformed to meet assumptions of RM ANOVA and ANOVA (e.g., normality, equal variance, compound symmetry) when necessary.

Lateral statistical analysis—The relationship between bat activity and aquatic insect availability with lateral distance from the river was examined using simple linear regression analysis. The effects of site type on insect abundance and biomass with distance from the river were examined using analysis of covariance (ANCOVA). Two ANCOVAs were conducted with aerial insect abundance and biomass as response variables, and site type and distance from the river as explanatory variables. Unfortunately due to a limited number of bat detectors, I was unable to collect replicated bat activity data at multiple sites within each site type along the lateral dimension. Thus, I only had sufficient replication to do ANCOVA for aerial insect abundance and biomass, and not bat activity. I am, however, able to show representative patterns of lateral bat activity for one river segment that included all 3 site types. By having all 3 site types along one contiguous river segment I avoid confounding site and site type. I was able to use negative exponential decay models to describe lateral declines in bat activity with distance from the river at each site type. 1-way ANOVA was used to compare area under each exponential decay curve among each site type. When necessary data were transformed to meet ANOVA and ANCOVA assumptions.

RESULTS

Longitudinal dimension bat activity and insect availability

Along the longitudinal dimension, I examined how riverine structure and trophic resources affected bat activity by measuring bat activity, bat density, and insect availability directly above the river at sites with variable channel confinement. I found that bat activity (Fig. 2) and bat density (Appendix C: Fig. 29) were significantly related to channel confinement. Here, I recorded significantly higher bat activity along confined reaches than unconfined reaches (simple linear regression, $R^2 = 0.31$, $F_{1,20} = 8.5$, $P = 0.01$). Using forward stepwise multiple regression analysis, channel confinement was the only explanatory variable to significantly predict bat activity ($R^2 = 0.36$, $P = 0.001$, n = 25) and bat density ($R^2 = 0.17$, $P = 0.04$, n = 25) along the longitudinal dimension while aquatic and terrestrial abundance and aquatic biomass were not included in the model. Further, bat activity and density were not related to aquatic insect abundance or biomass directly above the river during peak insect availability (July; Fig. 3; Appendix C: Figs. 30 and 31). In fact, bat activity was generally lower at sites with higher aquatic insect biomass (Fig. 3b). Thus, along a longitudinal dimension, riverine structure (channel confinement) had a stronger effect on bat activity and density than trophic resource availability directly above the river.

Bat activity was significantly higher above the river at confined sites in comparison to unconfined sites with and without alder (RM ANOVA, site type treatment effects, $F = 33.6$, df = 2, $P < 0.001$) but bat activity did not vary throughout the summer (RM ANOVA, sampling period treatment effects, $F = 2.7$, df = 2, $P = 0.11$; site type by sampling period treatment was not significant; Fig. 4a). Bat density did not vary among the different site types or over time (Appendix C: Table 22, Fig. 32).

Aquatic insect emergence rates ranged from 1.7 m^{-2} d^{-1} (unconfined with alder in May) to 36.9 m^{-2} d^{-1} (unconfined with alder in early July) but did not differ significantly among site type (RM ANOVA, site type treatment effect, $F = 1.1$, df = 2, $P = 0.42$; Fig. 4b). Further, channel width did not vary among site type (1-way ANOVA, $F = 0.74$, df = 2, $P = 0.52$) thus overall emergence was equivalent among site types. However, emergence rate did vary across sampling periods with significantly lower emergence in May and August than July sampling period (RM ANOVA, sampling date treatment effect, $F = 10.7$, df = 3, $P < 0.01$).

Aerial aquatic insect abundance and biomass were consistently higher than terrestrial insect abundance and biomass among the different site types and sampling periods except in May at the confined site type (Fig. 4c-d). Aerial aquatic and terrestrial insect abundance were not significantly different among site type or sampling date (RM ANOVA; site type treatment effect; aquatic insect abundance, *F* = 0.53, df = 1, *P* = 0.54; terrestrial insect abundance, *F* = 0.16, df = 2, *P* = 0.86; Fig. 4c). Aerial aquatic and terrestrial insect biomass followed a similar pattern with no significant differences among site type (RM ANOVA; site type treatment effect; aquatic insect biomass, *F* = 0.96, df = 2, *P* = 0.45; terrestrial insect biomass, *F* = 3.9, df= 2, *P* = 0.12; Fig. 4d). Aquatic insect biomass was, however, significantly higher in July in comparison to May and August sampling dates (RM ANOVA, sampling period treatment effect; aquatic insect biomass, *F* = 45.9, df = 2, *P* < 0.01) but not terrestrial insect biomass (RM ANOVA, sampling period treatment effect, terrestrial insect biomass: *F* = 6.3, df = 2, *P* = 0.06; Fig. 4d). See Appendix C for RM ANOVA tables.

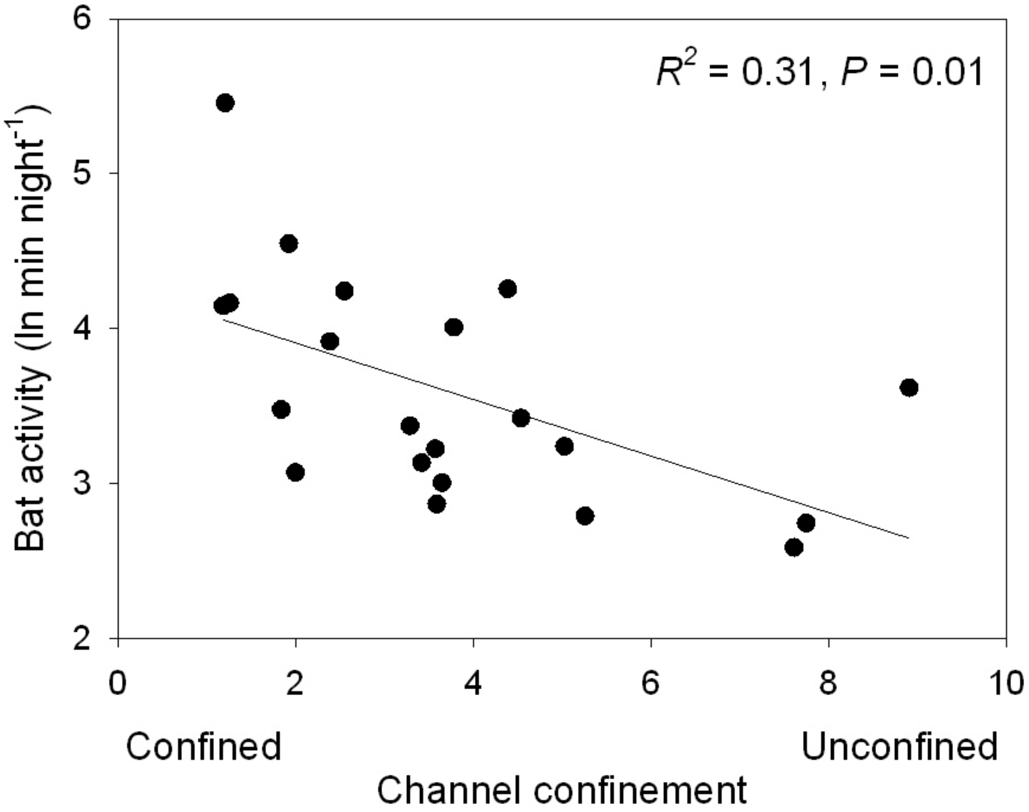

FIG. 2. Mean bat activity versus channel confinement. Channel confinement was measured as the ratio of valley floor width (m) to channel width (m). Channel confinement significantly decreased along the X-axis.

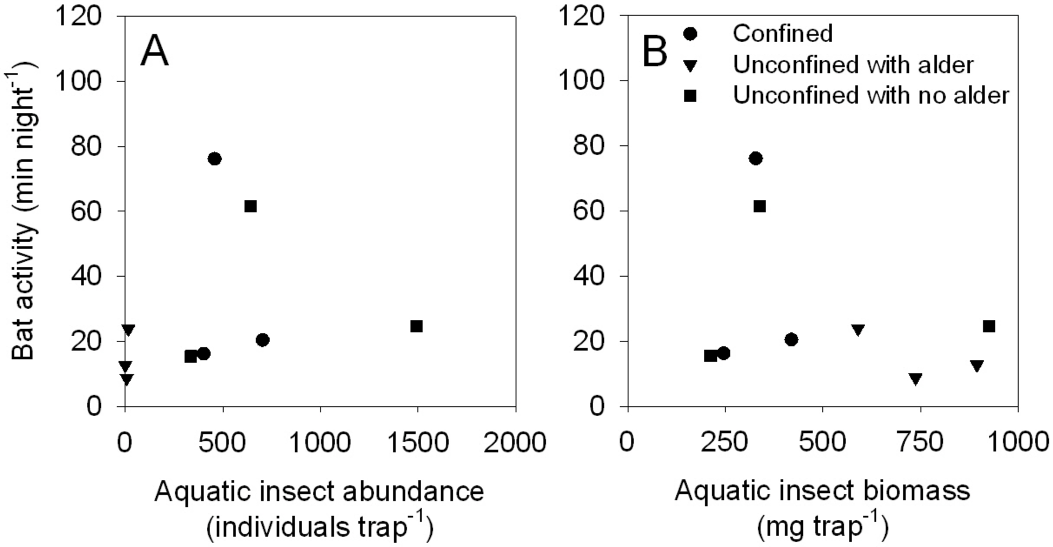

FIG. 3. Mean bat activity versus aquatic insect abundance (A) and biomass (B) directly above the river during peak emergence (July).

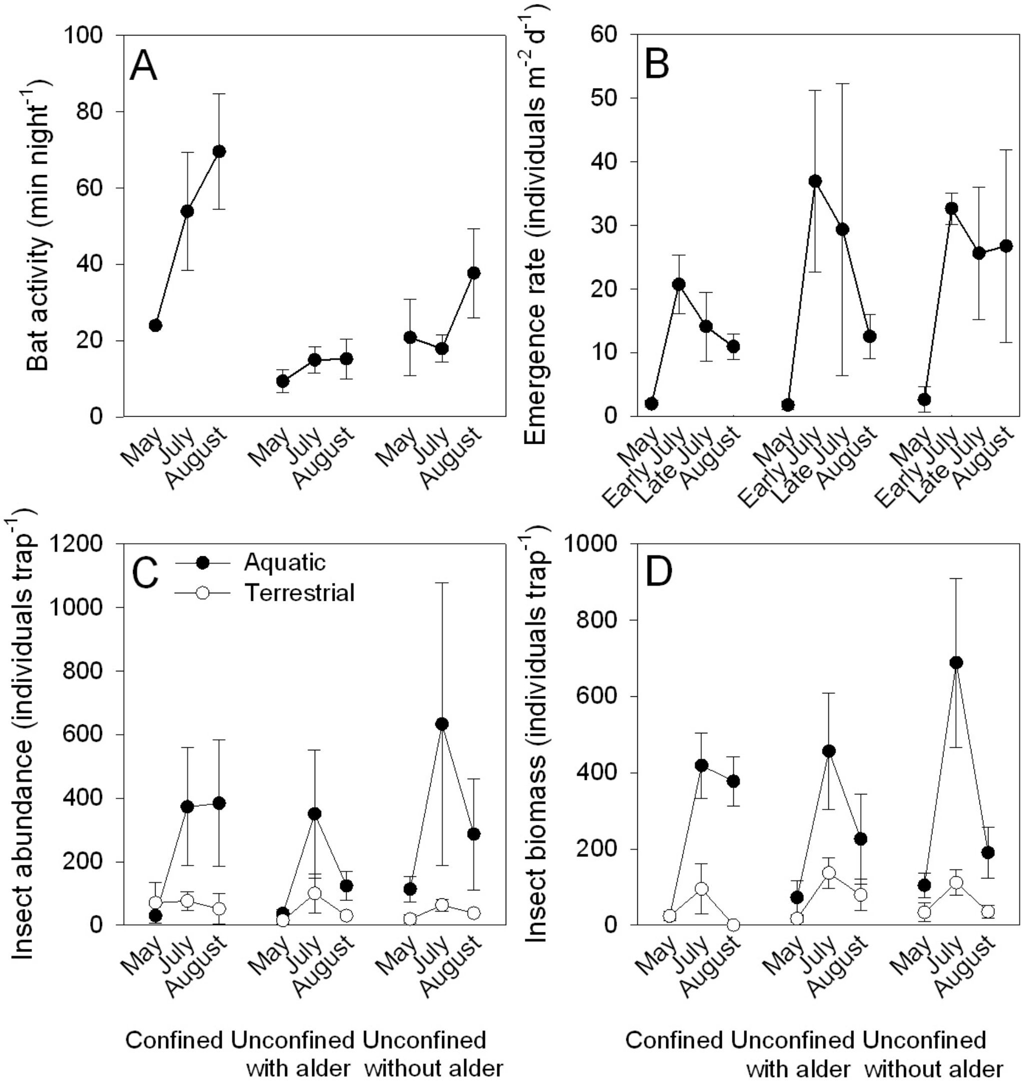

FIG. 4. Bat activity, aquatic resource emergence, and aquatic and terrestrial aerial insect availability directly above the river. Mean (± SE) bat activity (A) aquatic insect emergence rate (B), and aquatic (closed circles) and terrestrial (open circles) insect abundance (C) and biomass (D). Aquatic insect emergence rate was measured during 4 5-day sampling periods at each site type. Aerial insects were caught on sticky traps above the river during 3 5-day sampling periods at each site type.

Lateral dimension bat activity and insect availability

We examined the effects of riverine structure and trophic resource availability on bat activity along the lateral dimension by measuring bat activity and insect availability with increasing distance from the river at the three different site types (confined, unconfined with alder, and unconfined without alder). Along the lateral dimension, bat activity was positively related to aquatic insect abundance (linear regression, $R^2 = 0.69$, $F = 22.4$, n = 12, $P < 0.001$) and biomass (linear regression, $R^2 = 0.59$, $F = 14.1$, n = 12, $P = 0.004$) with distance from the river (Fig. 5). Bat density was also positively correlated with aquatic insect abundance (linear regression, $R^2 = 0.76$, $F = 31.6$, n = 12, $P < 0.001$) and biomass (linear regression, $R^2 = 0.50$, $F = 9.9$, n = 12, $P = 0.01$) with distance from the river (Appendix C: Table 23).

Aquatic insect abundance during peak insect availability (July) was concentrated directly above the river along the different site types and declined significantly with distance from the river (ANCOVA; distance treatment effect, $F = 11.7$, df = 1, $P = 0.001$; Appendix C: Table 24). However, site type did not have had a significant effect on the lateral dispersal of aquatic insect abundance into the terrestrial watershed (ANCOVA; site type treatment effect, $F = 0.75$, df = 1, $P = 0.40$). Terrestrial insect abundance did not vary with distance from the river or site type (Appendix C: Table 24). Similar to aquatic insect abundance, aquatic insect biomass declined significantly with lateral distance from the river but did not differ among site type (ANCOVA; distance site type treatment effect, $F = 4.4$, df = 1, $P = 0.04$; site type treatment effect, $F = 2.1$, df = 1, $P = 0.15$).

Terrestrial insect biomass was not related to distance or site type (Appendix C: Table 24). Insect availability followed a similar pattern with distance from the river during May and August sampling periods (Appendix C: Tables 25 and 26).

Similar to aquatic insect abundance and biomass, bat activity was highest directly above the river and declined with lateral distance into the terrestrial watershed regardless of site type (Appendix C: Fig. 33-35). Exponential decay models described bat activity well at the confined site ($R^2 = 0.91$, $n = 4$, $P = 0.046$) but not at the unconfined site with or without alder (Table 2). Bat activity was significantly higher directly above the river (0-m) at the confined sites in comparison to the unconfined sites (Fig. 4a), but the total area under each curve did not vary significantly among site type (1-way ANOVA, $F = 5.1$, df = 2, $P = 0.051$; data not shown).

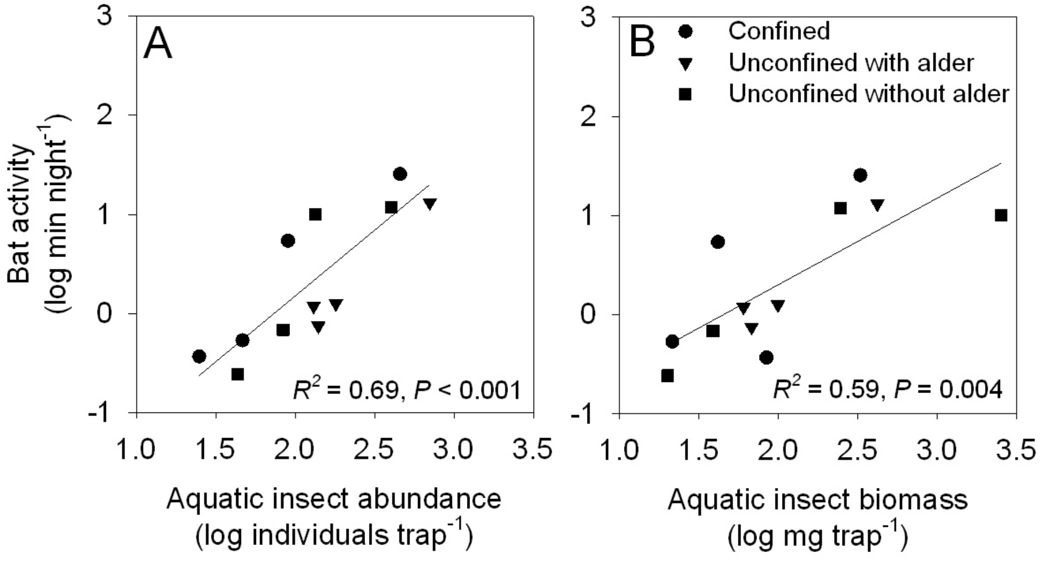

FIG. 5. Mean bat activity versus aquatic insect abundance (A) and biomass (B) with lateral distance from the river at each site type during peak insect abundance (July).

TABLE 2. Lateral declines in bat activity with distance from the river.

Site type	A	B	R^2	P
Confined	25.4 (2.9)	-1.11	0.91	0.046
Unconfined with alder	13.2 (5.6)	-0.70	0.86	0.074
Unconfined without alder	11.8 (1.0)	-0.95	0.71	0.159

Notes: A represents mean (± SE) bat activity (min/night) directly above the river, B describes the decay rate of bat activity with lateral distance from the river, R^2 refers to the fit of the exponential decay model at each site type, and P describes the significance level.

DISCUSSION

River to watershed exchange of riverine derived energy, nutrients, and organisms have profound effects on the distribution and abundance of terrestrial consumers in riparian ecosystems (Polis et al. 1997, Nakano and Murakami 2001, Sabo and Power 2002b, Paetzold et al. 2005). Aquatic resource subsidies also alter food-web structure in riparian ecosystems (Henschel et al. 2001, Henschel 2004, Baxter et al. 2005). My results suggest that the ability of a notably mobile consumer to track resources in watersheds is constrained by riverine landscape structure along the longitudinal dimension but not along the lateral dimension. Specifically, channel confinement is the best predictor of where bats congregate longitudinally along rivers, but resource availability has strong effects on the relative activity of bats laterally with reference to the active channel regardless of channel confinement.

Longitudinal bat activity

The results of this study suggest that rivers provide important foraging habitat to insectivorous bats and the location of bat activity is related to riverine landscape structure. Along the longitudinal dimension, channel confinement significantly predicted the location of bat activity but not insect availability. Here, bat activity was concentrated directly above the river along confined river reaches but not above unconfined reaches regardless of presence of riparian vegetation. Lower bat activity along unconfined sites than confined sites may be due to differences in proximity to roosting sites, turbulence of water flow, clutter associated with riparian vegetation along the river, or variation in trophic resource availability. Yet close proximity of sites (< 5 km) likely excludes proximity to roosting sites as a factor.

Water flow characteristics may vary along the gradient in channel confinement, as confined reaches tend to be associated with faster moving riffle habitat, while unconfined reaches tend to support slower moving pool habitat (Montgomery and Buffington 1997). Riffle versus pool habitats produce varying amounts of acoustic noise. Riffles, which are characterized by more turbulent water flow, produce higher acoustic interference than slow moving pool habitats. Several studies have shown that bats prefer river reaches with smooth flow versus turbulent surfaces, which has been attributed to high insect availability, reduced clutter, and lower ultrasonic noise that can interfere with prey detection and capture (Warren et al. 2000, Kusch et al. 2004). Von Frenkell and Barclay (1987) showed that the little brown bat (*Myotis lucifugus*) preferred pools to riffles when insect abundance did not differ among the habitat types. In the current study, presence of riffle and pool habitats occurred at a smaller spatial scale than variation in channel confinement, therefore, this factor likely does not explain variation in bat activity along the longitudinal gradient in channel confinement.

Longitudinal differences in bat activity may be due to variation in structural complexity associated with riparian vegetation. Lower bat activity along unconfined sites with alder vegetation than confined sites may have resulted from alder trees interfering with successful prey capture by hindering echolocation and by creating obstacles in the flight path (Mackey and Barclay 1989, Brigham et al. 1997). Several studies have shown that bats prefer environments with low structural clutter compared to those with high structural clutter (Brigham et al. 1997, Erickson and West 2003, Sleep and Brigham 2003). For example, Loeb and O'Keefe (2006) documented high bat activity in areas with low-density vegetation in comparison to high-density forests. Thus, high bat activity along confined sites in comparison to unconfined sites with alder was likely due to low clutter caused by reduced vegetation structure.

Bat activity was not related to trophic resources along the longitudinal dimension. While aquatic and terrestrial insect availability did not vary among site type when measured ~1 m above the river, vertical variation in insect availability may have existed. Specifically, confined reaches may limit aquatic insects to directly above the river, while unconfined reaches without alder vegetation may promote the lateral flow of aquatic resources further into the watershed. Studies show that river channel geomorphology affects the penetration of aquatic insects into terrestrial ecosystems (Iwata et al. 2003, Iwata 2007). Further, these studies suggest that river-channel geomorphology likely contributes to potential hotspots for terrestrial-consumer foraging activity. Thus, it is not surprising that channel confinement is related to longitudinal variation in bat activity and density. Future studies of bat-foraging activity would benefit from consideration of variation in bat activity and insect availability along the vertical dimension.

Lateral bat activity

In contrast to the lack of strong relationships between trophic resources and bat activity along the longitudinal dimension, aquatic insect resource availability was significantly related to bat activity along the lateral dimension. Here, bat activity seemed to track lateral declines in aquatic insect resource availability with distance from the river (Fig. 5). Not surprisingly, terrestrial insect availability did not vary with distance from the river. Further, channel confinement and riparian vegetation did not affect lateral dispersal of aquatic insects (Appendix C: Fig. 36). However, lower negative decay values at the unconfined site with alder in comparison to the confined and unconfined without alder sites further suggest that riparian vegetation may hinder bats from tracking aquatic resources laterally. Unfortunately, I only measured lateral patterns in bat activity along a single ~700-m reach of river. Thus, I cannot generalize the effects of aquatic insects and riparian vegetation beyond this single river reach. However, combined with insect data from 9 sites along a ~5-km river segment, these data do provide evidence that aquatic insect abundance and biomass but not riverine landscape structure are related to lateral patterns in bat activity. This is not surprising as Fukui et al. (2006) found that experimental reduction of aquatic insect emergence significantly reduced bat activity along a forest stream in the spring during peak aquatic insect availability. Along the South Fork Eel River, bat activity was highest directly over the river and had substantially decreased by 25-m from the river in all site types. Aquatic insects, which make up a large proportion of bat diet (Belwood and Fenton 1976), were also significantly higher above the river than in the terrestrial watershed. Thus, along the lateral dimension, bats seemed to track aquatic insect availability but did not respond to variation in landscape structure or terrestrial insect resources.

Conclusions

The results of this study suggest that the effects of riverine landscape structure and prey availability largely depend on the dimension of interest. Along a river's longitudinal axis, landscape structure rather than trophic resources predicted bat activity most strongly. By contrast, trophic resources became more important when considering lateral exchanges between aquatic and terrestrial watersheds. Bats track aquatic insect availability from river to ridge in spite of local valley constraints. One notable exception to this conclusion is that riparian vegetation appears to hinder the ability of bats to track aquatic insect availability laterally.

Bat populations are declining worldwide. Nearly 21% of the world's bat species are considered threatened and an addition 23% are considered near threatened (Hutson et al. 2001), largely due loss of foraging and roosting habitat. Here I show that rivers and riparian areas provide important bat foraging habitat and that reaches with confined channels are particularly attractive foraging sites for bats for reasons unrelated to resource supply. This is not surprising as river channel geomorphology and vegetation structure have been show to have both direct and indirect effects on biological patterns and processes (Frissell et al. 1986, Ward 1998, Robinson et al. 2002). To improve the status of these ecologically important species, it is critical that these biological hotspots be considered and protected in habitat conservation planning efforts. Moreover, many of the bat species that forage in confined reaches along the South Fork Eel River roost in tree cavities, caves, and rock outcrops in upland habitats. Thus, protection of riverine habitats alone is not enough protect these species. Rather, bat conservation and management plans should include the protection of both riverine and upland habitats.

CHAPTER 3

INFLUENCE OF RIVER DRYING AND INSECT AVAILABILITY ON BAT ACTIVITY ALONG THE SAN PEDRO RIVER, ARIZONA (USA)

Abstract. I examined the effects of flow permanence and prey resource availability on bat activity along a desert river in southeastern Arizona. Bats use desert rivers for foraging and drinking. Here I evaluated the consequences of flow reduction and drying on prey resource availability and bat activity. To do so I sampled bat activity and insect availability during the dry season at perennial and intermittent sites along the San Pedro River. Intermittent sites included both flowing and dry conditions during the study period. Bat activity significantly declined between May and June sampling periods but was not related to whether sites had perennial or intermittent flow. Declines in summer bat activity corresponded to reductions in insect availability during the same period, but only at perennial sites. Bats tracked aquatic insect availability at perennial sites but not at intermittent sites, where insects actively aggregated above localized wet portions of the intermittent reaches. Rather, bats were responding to higher terrestrial insect availability when surface flows declined at intermittent sites. Finally, both bat and insect availability declined to nearly undetected levels when the river dried at 2 of 16 sites. Thus, intermittency affects bat foraging activity indirectly via its effects on prey availability. Seasonal river drying appears to have complex effects on foraging decisions by bats, initially causing imperfect tracking by consumers of localized concentrations of resources, but later resulting in disappearance of both insects and bats after complete drying.

INTRODUCTION

Bat populations are declining worldwide. As a result of habitat loss, exposure to pesticides and pollution, human disturbance, and disease, approximately 22% of bat species are considered threatened and an additional 23% are listed as near threatened (Hutson et al. 2001, Frick et al. 2010). Management and protection of critical bat habitat is essential to managing bat populations and preserving high faunal diversity.

Rivers and riparian areas are particularly important habitat for insectivorous bats (Walsh and Harris 1996, Grindal et al. 1999, Law and Chidel 2002, Fukui et al. 2006, Rogers et al. 2006, Williams et al. 2006). High rates of insectivorous bat foraging activity along waterways may be a consequence of aggregations of emergent aquatic insects over river corridors, which provide an important food source to many bat species (Fukui et al. 2006). While a few studies have examined bat activity along desert river and riparian areas (e.g., Rogers et al. 2006, Williams et al. 2006), almost nothing is known about how changes in the flow regime and in particular, the flow permanence of a river, affects bat foraging activity and abundance.

Increasingly, human activities are contributing to drying of rivers, including large rivers, such as the Yellow River in China and the Colorado River in Arizona, USA that did not dry historically (e.g., Zusman 2000, Pearce 2006, Stone and Jia 2006). Perennial water sources in arid and semiarid regions provide particularly critical foraging habitat for bats due to scarce water availability in these areas. Yet increased demand for surface and groundwater resources by growing human populations are threatening perennial surface flows in the arid southwestern United States. In fact, many perennial rivers have recently become intermittent or ephemeral due to groundwater pumping, dams, and stream diversions (Gleick 2003, Pearce 2006).

Reduction of surface flow can have both direct and indirect effects on aquatic organisms. Direct effects include loss of water and flow, reduction of habitat availability, and loss of stream connectivity, while indirect effects include reduction in water quality, changes in food resource availability, altered community composition and changes in species interactions (Closs and Lake 1994, Lake 2003). For example, several studies have shown a decrease in larval aquatic insect densities following reductions in surface flows (e.g., Cowx et al. 1984, Wood et al. 2000). Decreases in larval aquatic insect densities may be due to increased competition and predation as habitat availability and food quality and quantity decline (McIntosh et al. 2002). Other studies have shown increases in aquatic insect densities during low-flow conditions as aquatic insects become concentrated in isolated pools (Gore 1977, Wright and Berrie 1987, Stanley et al. 1994). Variable responses to reductions in surface-water flows are likely related to the extent and duration of river drying.

Numerous studies have focused on how aquatic organisms, primarily aquatic insects and fish, respond to reductions in surface-water flow (e.g., Lake 2003, Dewson et al. 2007); however, only a few studies to date have examined the consequences of alterations to the hydrologic regime on terrestrial predators that are dependent on surface-water flows (Brand et al. 2008, Paetzold et al. 2008, McCluney and Sabo 2009, Brand et al. 2010b). Alterations of the hydrologic regime likely have consequences for insectivorous bats, which depend on surface flows for drinking and foraging habitat, and on riparian vegetation for roosting habitat.

Our primary research objective was to examine the effects of declining surface flows and river drying events on insect prey availability and consequently on bat foraging activity along the San Pedro River in southeastern Arizona. This river maintains perennial flow in much of its upper watershed (The Nature Conservancy 2008); however, regional groundwater declines, regional drought, and localized groundwater pumping have caused some sections of the San Pedro River that were once perennial to become intermittent and even ephemeral (Leenhouts et al. 2006). River drying events are occurring with increasing frequency along the San Pedro River; largely due regional groundwater declines and localized groundwater pumping from the alluvial aquifer (Stromberg et al. 1996, Mac Nish et al. 2009, Brand et al. 2010a). First I investigated how changes in hydrologic regime and the reduction of surface-water flow along intermittent reaches affected the location of bat foraging activity. Drinking water is an important resource to foraging bats; therefore, I predicted that bat activity would be highest at perennial versus intermittent sites and at intermittent sites when they were flowing (vs. dry). Second, I examined how insect availability influenced bat activity. Insects provide an important food resource for foraging bats. Thus, I predicted that bats would “track” the abundance or biomass of insects, regardless of surface-water presence.

METHODS

Study Site

The San Pedro River flows north from Sonora, Mexico, into southeastern Arizona, USA, and is one of the last entirely free flowing rivers in the arid Southwest. In 1988, Congress designated a 50-km section of the upper San Pedro River as a National Conservation Area. In this area, livestock and grazing, off road vehicle use, sand and gravel mining, floodplain agriculture, and groundwater pumping are no longer permitted (Yuncevich 1993, Krueper et al. 2003).

The San Pedro River valley supports 24 species of bats (Hanson 2001), comprising more than half of the species of bats found in the United States and Canada (Nowak 1994). In addition to high bat diversity, the San Pedro River valley is a rare remnant of the Fremont cottonwood-Goodding willow (*Populus fremontii* and *Salix gooddingii*) gallery forest type, which is declining in many places throughout the arid Southwest in response to extensive groundwater declines and flood alteration (Stromberg 2007), but increasing along a few rivers including the upper San Pedro River (Webb and Leake 2006, Stromberg et al. 2010).

In 2007 annual precipitation in the San Pedro River basin was 29.3 cm and 53% of its annual precipitation occurred during the summer monsoon (July – September; USGS gauge 09471000 San Pedro River at Charleston, AZ). This reflects a typical year, with moderate and consistent flows during the winter wet season (December – March), low flows during the spring and summer dry season

(April – June), and high and variable flows during the summer monsoon (July - September; Hirschboeck 2009).

Forest structure of the upper San Pedro River riparian zone varies along gradients of groundwater and stream flow, allowing designation of riparian "condition classes" indicative of linked changes in vegetation and hydrology (Leenhouts et al. 2006, Stromberg et al. 2006). Reaches with perennial flow and shallow groundwater are characterized by well-developed, multi-aged cottonwood-willow forests ("perennial" condition class). Tamarisk (*Tamarix ramosissa*), if present, is subdominant and herbaceous plant cover lines the river channel. Where flow is intermittent but frequent ("intermittent" condition class), tamarisk presence increases but cottonwood-willow forest remains abundant. Herbaceous cover is reduced and is replaced by more drought-tolerant species (e.g., Bermuda grass, *Cynodon dactylon*). Tamarisk has largely replaced cottonwood-willow forest along reaches that have highly intermittent flow and sharply seasonally declining water tables ("dry" condition class). Herbaceous cover is sparse along these intermittent-dry sections of the river. As of 2006, more than 39% of the conservation area was classified as "perennial" and 55% was classified as "intermittent" condition class (Leenhouts et al. 2006, Stromberg et al. 2006); however, the spatial extent of surface flow during the dry season varies widely among years.

To examine how surface-water flow and insect availability influence bat foraging activity, I made use of natural variation in these factors along a ~100 km reach of the San Pedro River. I selected 16 sites, 13 of which were located within the National Conservation Area and 3 of which were located on Three Links Farm, a river preserve owned by The Nature Conservancy since 2002, when groundwater pumping ceased and perennial flows were restored to a six-mile section of the river. Sites, each 100-m long, were assigned to a condition class according to Leenhouts et al. (2006). Of the 16 study sites, 8 were classified as perennial and 8 were considered intermittent (Fig. 6, Table 3). Perennial sites flowed year round, while intermittent sites flowed the majority of the year but typically dried during the summer. Five of the 8 intermittent sites had surface flow during my study. Dry sites were not included in this study due to limited access to this condition class. This study was conducted during the summer dry season (May – June) prior to monsoon storms and floods.

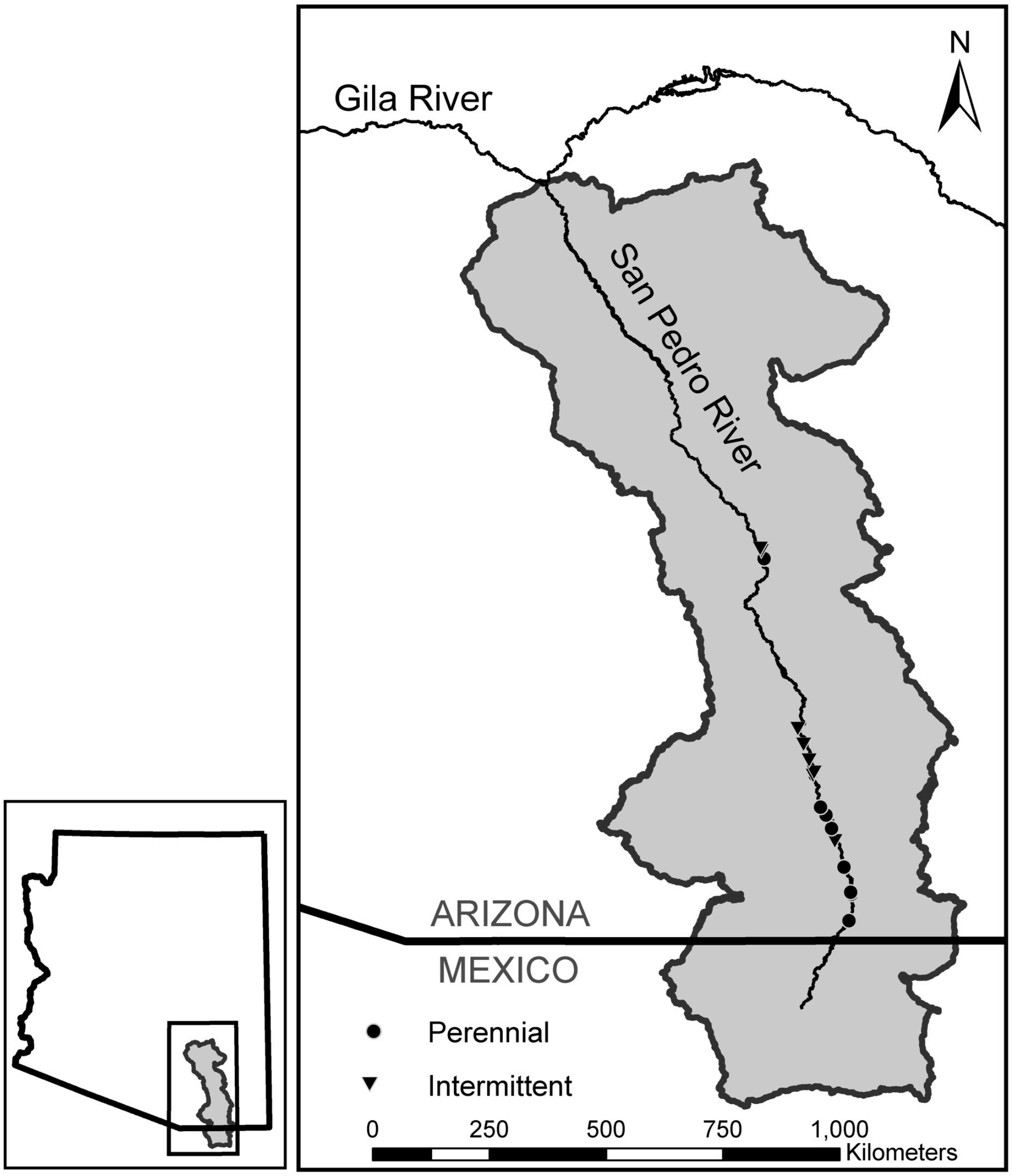

FIG. 6. Study site locations along the San Pedro River.

TABLE 3. Study site condition class, and flow condition during sampling period.

Site name	Condition class	May	June
Palominas	Perennial	Wet	Wet
Hereford - South	Perennial	Wet	Wet
Hereford - North	Perennial	Wet	Wet
Cottonwood	Perennial	Wet	Wet
San Pedro House	Intermittent	Wet	Wet
Lewis Springs	Perennial	Wet	Wet
Grayhawk Nature Center	Perennial	Wet	Wet
Charleston	Perennial	Wet	Wet
Boquillas - South	Intermittent	Wet	Wet
Boquillas Ranch	Intermittent	Wet	Dry
Fairbank	Intermittent	Wet	Dry
Contention	Intermittent	Dry	Dry
Summer	Intermittent	Wet	Wet
Three Links Farm - South	Perennial	Wet	Wet
Three Links Farm - Road	Intermittent	Wet	Wet
Three Links Farm - North	Intermittent	Wet	Wet

Insect availability

Insect availability was measured 3 ways: aquatic insect emergence rate; aerial aquatic, terrestrial, and total (aquatic and terrestrial) insect abundance; and aerial aquatic, terrestrial, and total insect biomass. Measurement of insect availability coincided with bat acoustic monitoring. Aquatic-insect emergence was measured using triplicate, 0.25-m^2 floating emergence traps, deployed at each site for 5 days in May and June. After 5 days, insects collected in emergence traps were preserved in ethanol until processed.

Aerial aquatic, terrestrial, and total insect abundance was measured at each site using replicate sticky traps (n = 3) attached to rebar directly above the active river channel, deployed for 5 days in May and June. Sticky traps consisted of transparency film (603.2 cm^2) coated with Tangle-Trap adhesive (Tanglefoot, Grand Rapids, Michigan, USA). Upon collection, sticky traps were covered with cellophane and frozen until insects were processed in the lab. Insects on sticky traps were subsampled using a 2.54 cm X 2.54 cm grid. All insects, in 10 randomly selected squares, were identified to order, except for Dipterans and Coleopterans, which were identified to family according to Borror et al. (1989) and Merritt et al. (2008). Insects were categorized as aquatic or terrestrial based on order and Diptera and Coleoptera family classification. Aquatic, terrestrial, and total insect abundance was recorded for the 10 squares and multiplied by 9.35 to estimate insect abundance for the entire sticky trap. Length of subsampled insects was measured (±1 mm) using a Leica S6D dissecting microscope, and biomass was calculated from length-mass regressions (Sabo et al. 2002).

Bat activity

Bat activity was measured acoustically using Anabat II bat detectors (Titley Electronics, Ballina Australia) connected to zero-crossings analysis interface modules (Anabat CF Storage ZCAIM). Bat activity was measured using 4 bat detectors that were moved among the 16 sites within two 12-day periods in May and June 2007. At each site, bat activity was recorded from dusk until dawn, for three consecutive nights each month. Bat detector microphones were oriented at an angle of 45° upwards (O'Farrell 1998) and were calibrated at the beginning and end of the study. Bat detectors could detect bat activity up to 9 m from the detector.

Bats emit different call types depending on the species, the phase of prey capture, and the foraging environment (Kalko and Schnitzler 1993). Echolocation calls can be divided by call structure into frequency modulated (FM) or constant frequency (CF) calls. Bats that forage within cluttered environments (dense vegetation) tend to emit FM calls, while bats that forage within open environments emit CF calls (Schnitzler and Kalko 2001). Based on variation in call characteristics, bat calls were placed into ecomorphological functional groups, defined as groups of bats with similar characteristics that tend to be associated with different habitat use and food resource partitioning (Aldridge and Rautenbach 1987, Saunders and Barclay 1992). Bat calls with a minimum frequency (Fmin) > 35 kHz were considered high-frequency bats and calls with a Fmin < 35 kHz were categorized as low-frequency bats. Bat calls were also separated based on call duration. Bat calls with a duration < 6 ms were categorized as FM calls and calls with a duration > 6 ms were categorized as CF calls. This resulted in 4 ecomorphological groups: high FM, low FM, high CF, and low CF (Table 4). Recorded bat calls were analyzed and placed into ecomorphological groups using Analook Bat Call Analysis System (Version 4.9g) and Microsoft Access software. Only calls with > 2 pulses were categorized into ecomorphological functional groups. Calls were placed into an ecomorphological group when > 75% of the call pulses met the criteria for that group. Bat activity is reported as mean minutes of bat activity per night.

TABLE 4. Bat species found along the San Pedro River and assigned ecomorphological group.

Common name	Species name
High-frequency modulated	
Mexican long-tongued bat	*Choeronycteris mexicana*
Lesser long-nosed bat	*Leptonycteris curasoae*
California leaf-nosed bat	*Macrotus californicus*
Southwestern myotis	*Myotis auriculus*
California myotis	*Myotis californicus*
Small-footed myotis	*Myotis ciliolabrum*
Cave myotis	*Myotis velifer*
Long-legged myotis	*Myotis volans*
Yuma myotis	*Myotis yumanensis*
Western pipistrelle	*Pipistrellus hesperus*
Low-frequency modulated	
Townsend's big-eared bat	*Corynorhinus townsendii*
Spotted bat	*Euderma maculatum*
Fringed myotis	*Myotis thysanoides*
High-constant frequency	
Red bat	*Lasiurus blossevillii*
Low-constant frequency	
Pallid bat	*Antrozous pallidus*
Big brown bat	*Eptesicus fuscus*
Western mastiff bat	*Eumops perotis*
Allen's big-eared bat	*Idionycteris phyllotis*
Silver-haired bat	*Lasionycteris noctivagans*
Hoary bat	*Lasiurus cinereus*
Southern yellow bat	*Lasiurus xanthinus*
Pocketed free-tailed bat	*Nyctinomops femorosacca*
Big free-tailed bat	*Nyctinomops macrotis*
Mexican free-tailed bat	*Tadarida brasiliensis*

Statistical analysis

The effects of flow-class condition on insect availability and bat activity were examined over time using repeated-measures analysis of variance (RM ANOVA). Response variables were bat activity, aquatic insect emergence, and aquatic, terrestrial, and total insect abundance and biomass, and total, high-FM, low-FM, high-CF, and low-CF bat activity (12 separate tests) and the explanatory variables were condition class and month. When necessary, data were transformed to meet standard parametric assumptions of normality and equal variance, and Greenhouse Giesser-corrected degrees of freedom were used in the estimation of F-values for the fixed effect of interest (flow-class condition) to adjust for departures from sphericity. RM ANOVA tables are reported in Appendix D: Tables 27 and 28. Relationships between bat activity and insect availability were explored using regression analysis.

The effects of discrete river drying events on bat activity and insect availability were examined at two sites: Fairbank and Boquillas Ranch. Observed river drying events at these sites between May and June provided an opportunity to examine the punctuated effects of discrete drying events on the activity of bats. As described above, bat activity was measured on 3 consecutive nights when the river was flowing in May and 3 consecutive nights after the river had dried in June. Insect abundance and biomass were measured on 3 replicate sticky traps left out for 5 days at each site in May and June. With only two sites, statistical analysis of these effects was not valid, thus I present the results for these important point observations of drying graphically and discuss their implications and the limitations of their interpretation.

RESULTS

Insect availability

At all sites and all sampling times, aquatic insect abundance was higher than terrestrial insect abundance whereas terrestrial insect biomass was consistently higher than aquatic insect biomass. Aerial insect abundance was primarily composed of aquatic insects, mainly small Diptera and Ephemeroptera, while aerial insect biomass was dominated by terrestrial insects including Coleoptera and Hymenoptera (Table 5). Emergence was dominated by Diptera (Table 5). Aquatic insect abundance significantly declined over time at perennial and intermittent sites but terrestrial insect abundance did not vary throughout the dry season.

TABLE 5. Percentage abundance and biomass of major orders of insects collected on sticky traps and percentage of major orders of insects collected in emergence traps.

	Abundance				Biomass				Emergence			
	Perennial		Intermittent		Perennial		Intermittent		Perennial		Intermittent	
Order	May	June	May	June	May	June	May	June	May	June	May	June
Adult aquatic insects												
Diptera	63.26	67.83	31.53	29.19	37.40	16.57	63.69	43.16	77.93	78.05	79.47	62.97
Ephemeroptera	11.96	10.43	5.77	3.31	5.45	4.88	13.28	11.42	2.21	3.18	10.92	12.84
Trichoptera	0.08	0.21	0.02	0.05	0.01	0.06	0.07	0.24	0.88	1.28	0.86	0.41
Coleoptera	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	13.26	5.31	5.44	18.03
Hemiptera	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	4.61	9.74	2.50	3.69
Hymenoptera	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.80	1.76	0.81	2.06
Odonata	0.02	0.03	0.05	0.10	0.00	0.00	0.00	0.00	0.30	0.68	0.00	0.00
Plecoptera	0.00	0.00	0.00	0.00	0.01	0.02	0.01	0.02	0.00	0.00	0.00	0.00
Neuroptera	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.11	0.00	0.00	0.00	0.00
Aerial terrestrial insects												
Coleoptera	15.78	16.04	49.40	42.86	47.48	60.80	17.55	39.01				
Thysanoptera	6.56	2.23	1.08	0.40	0.59	0.18	3.79	1.26				
Homoptera	1.01	0.59	0.43	0.23	0.19	0.24	0.58	0.71				
Hymenoptera	0.90	2.01	9.99	19.89	7.41	11.53	0.76	1.30				
Hemiptera	0.40	0.31	1.26	0.97	0.58	0.50	0.20	0.16				
Lepidoptera	0.03	0.29	0.46	2.74	0.89	1.26	0.04	0.05				
Orthoptera	0.00	0.03	0.00	0.16	0.00	0.00	0.00	0.00				
Diptera	0.00	0.00	0.00	0.00	0.00	3.95	0.00	2.57				
Total aquatic insects	75.33	78.50	37.38	32.66	42.86	25.49	77.06	54.94				
Total terrestrial insects	24.67	21.50	62.62	67.35	57.14	78.47	22.94	45.06				

Bat activity

Bat activity declined from May to June at all 16 sites (RM ANOVA, between subjects or time effect, $F_{1,7} = 30.6$, $P = 0.001$); however, bat activity did not differ significantly between perennial and intermittent sites and there was no time by treatment effect. Bat activity was 3.1 times higher at perennial sites and 4.1 times higher at intermittent sites in May when flows were present at 7 of 8 intermittent sites than in June when flows were reduced at all sites and the river was dry at 3 of 8 intermittent sites (Table 3, Fig. 7a). Aquatic insect availability followed a similar pattern, with significantly higher aquatic insect abundance (RM ANOVA, time effect, $F_{1,5} = 8.6$, $P = 0.03$) in May than June. Aquatic insect abundance was highest at the intermittent sites in May and lowest at perennial sites in June (Fig. 7c). Aquatic insect abundance was not related to condition class. Aquatic insect emergence, aquatic insect biomass, and terrestrial and total insect abundance and biomass did not vary between sampling period or condition class (Figs. 7b and 7d; Appendix D: Figs. 38 and 39).

Bat activity in high-FM, low-FM, and low-CF ecomorphological functional groups was significantly higher in May than June (RM ANOVA, time effect; high FM: $F_{1,7} = 32.2$, $P = 0.001$; low FM: $F_{1,7} = 20.1$, $P = 0.003$; low CF: $F_{1,7} = 7.0$, $P = 0.03$; Fig. 8a, 8c, and 8d) but not related to condition class. There was a significant time by treatment effect for low FM bat activity ($F_{1,7} = 7.6$, $P = 0.03$). High-CF bat activity was not related to condition class or month (Fig. 8b).

Regression analysis showed that bat activity was significantly related to insect availability throughout the study (Table 6). In May, bat activity increased with total insect abundance but not aquatic or terrestrial insect abundance or biomass (Table 6). Low-CF bat activity in the same month was significantly related to terrestrial insect abundance and biomass. In June, bat activity and low-CF bat activity were related to aquatic insect biomass and abundance, respectively. At perennial sites, bat activity increased with terrestrial insect abundance, and total insect abundance and biomass. High-FM bat activity was also positively related to terrestrial insect abundance at perennial sites. Low-FM bat activity was significantly related to aquatic, terrestrial, and total insect abundance, and total insect biomass at perennial sites. In contrast to perennial sites, there was not a significant relationship between bat activity and insect availability at intermittent sites.

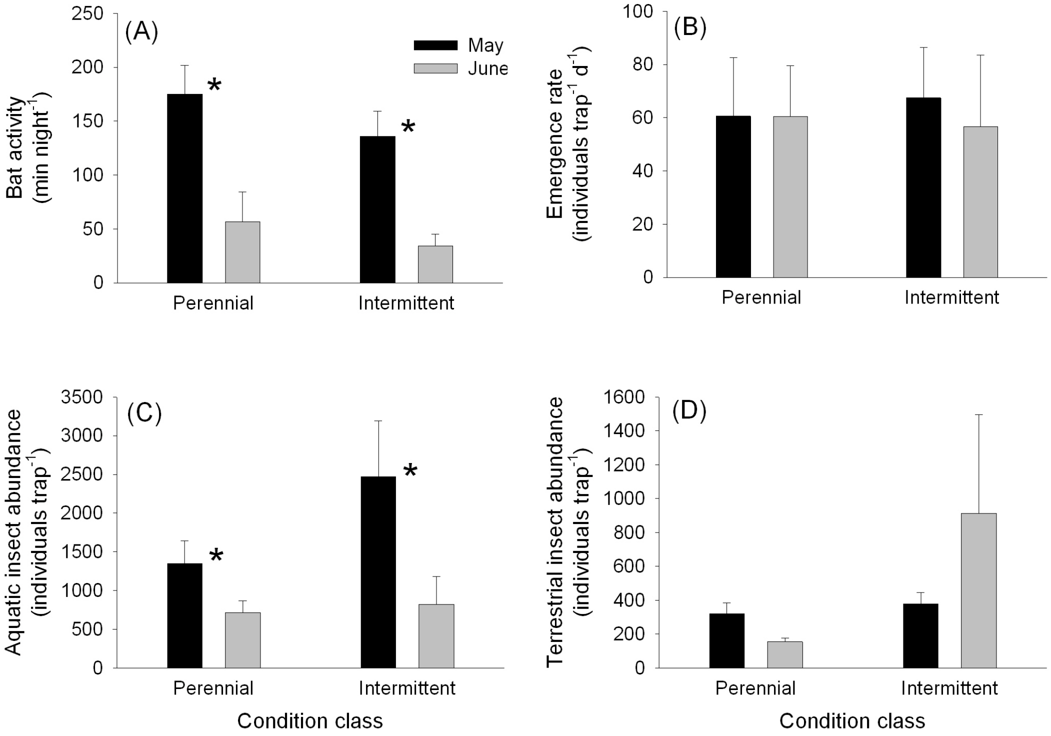

FIG. 7. Mean (± SE) bat activity (A), emergence (B), and aquatic (C) and terrestrial (D) insect abundance at sites in perennial and intermittent condition classes. Asterisks indicate significant differences between May and June bat activity and insect availability (RM ANOVA, $P < 0.05$).

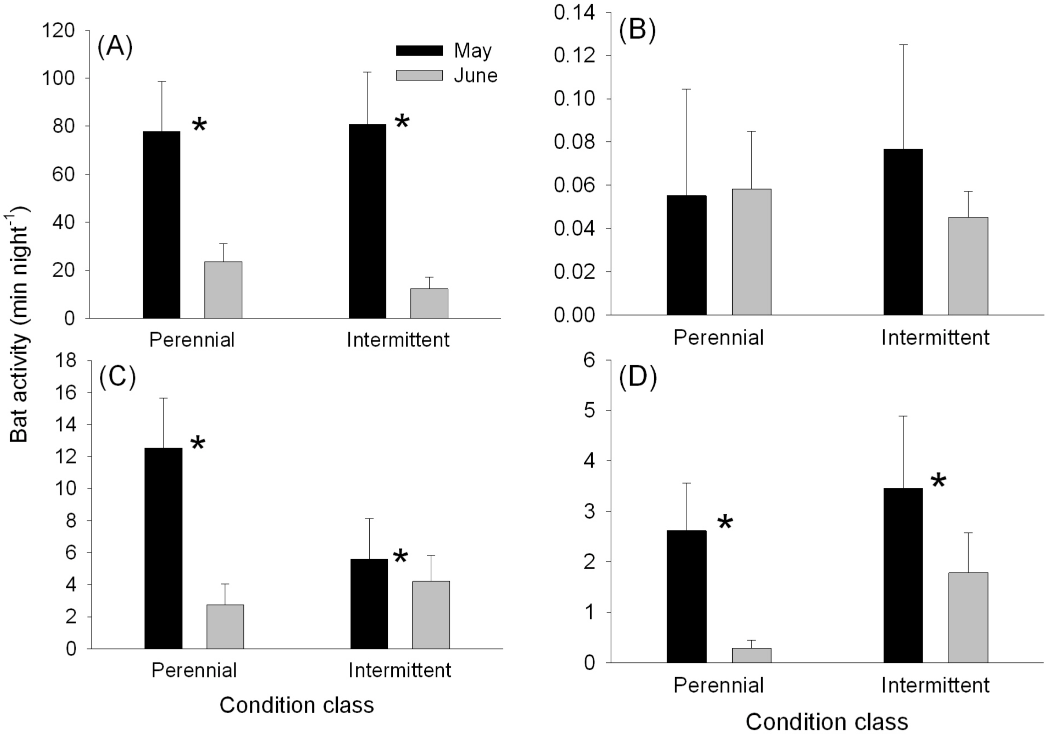

FIG. 8. Mean (± SE) bat activity by high-FM (A), high-CF (B), low-FM (C), and low-CF (D) ecomorphological functional groups at sites in perennial and intermittent condition classes. Asterisks indicate significant differences between May and June bat activity (RM ANOVA, $P < 0.05$).

TABLE 6. Results from linear regression analysis showing significant correlations between bat activity and insect availability.

Dependent variable	Independent variable		N	R^2	F	P
Bat activity	Total insect abundance	May	16	0.26	4.98	0.043
Low-CF bat activity[a]	Terrestrial insect abundance	May	16	0.29	5.63	0.033
Low-CF bat activity[a]	Terrestrial insect biomass	May	16	0.26	5.02	0.042
Low-CF bat activity[b]	Aquatic insect abundance	June	14	0.51	12.38	0.004
Bat activity[a b]	Aquatic insect biomass	June	14	0.31	5.28	0.040
Bat activity[a]	Terrestrial insect abundance	Perennial	16	0.33	6.84	0.020
Bat activity[a]	Total insect abundance	Perennial	16	0.29	5.75	0.031
Bat activity[a]	Total insect biomass	Perennial	16	0.35	7.46	0.016
High-FM bat activity[a]	Terrestrial insect abundance	Perennial	16	0.36	7.94	0.014
Low-FM bat activity[a]	Aquatic insect abundance	Perennial	16	0.34	7.19	0.018
Low-FM bat activity[a]	Terrestrial insect abundance	Perennial	16	0.28	5.33	0.037
Low-FM bat activity[a]	Total insect abundance	Perennial	16	0.44	10.78	0.005
Low-FM bat activity[a]	Total insect biomass	Perennial	16	0.38	8.38	0.012

[a] Data were ln transformed to meet assumptions of linear regression analysis (e.g., normality, equal variance)

[b] Sticky traps were lost at two sites, Contention and Summer, during June sampling period.

River drying

At the two sites that dried between the May and June sampling periods, total and high-FM bat activity were both considerably higher prior to river drying (Fig. 9a). Low-CF and low FM bat activity declined slightly following drying, and high-CF bat activity was close to zero during both wet and dry flow conditions. Aquatic insect abundance and biomass and total insect abundance were higher during May than during the no-flow conditions of June, while terrestrial insect abundance and biomass and total insect biomass were higher in June than in May (Fig. 9b).

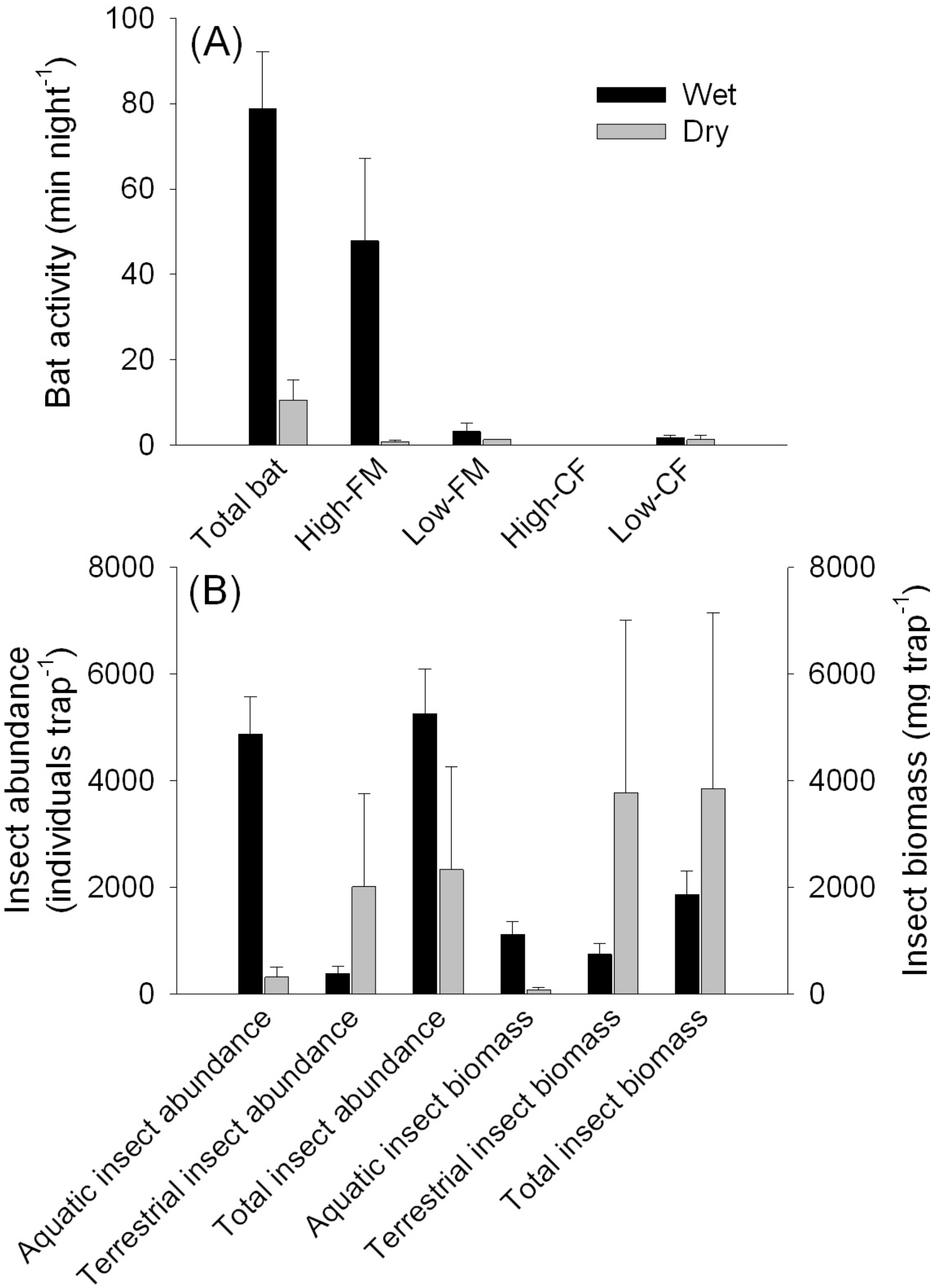

FIG. 9. Mean (+ SE) bat activity (A) and insect availability (B) during wet and dry flow conditions. Standard errors are estimated via temporal variation in bat activity over 3 consecutive nights. Standard error in insect abundance and biomass are estimated via spatial variation (3 sticky traps at each study site).

DISCUSSION

Periods of low flow or complete drying are a natural occurrence in many desert rivers (Stanley et al. 1997); however, human activities such as groundwater pumping and diversion dams have extended the occurrence, duration, and extent of no and low flow conditions in desert rivers. Groundwater and surface water decline have significantly altered river and riparian ecosystems in the southwestern United States (e.g., Lite and Stromberg 2005). Specifically, localized groundwater pumping and river dewatering have altered the natural hydrologic regime in the San Pedro River (Webb and Leake 2006, Stromberg and Tellman 2009). The frequency of river drying has increased along the San Pedro River (McKinnon 2007, Mac Nish et al. 2009), resulting in water scarcity for both aquatic organisms and terrestrial predators.

I examined how reductions in surface-water flow and changes in insect prey availability affected insectivorous bat foraging activity. I found that bat activity significantly declined during the dry season but that bat activity was not related to perennial or intermittent condition class classification. Instead, bat activity was related to insect availability, but only at perennial sites. Moreover, aquatic insect abundance declined throughout the dry season irrespective of flow condition, while terrestrial insect abundance increased at dry intermittent sites. Collectively, these results suggest that intermittency plays a strong role in determining bat distributions and foraging activity but this effect is indirect via the effects of flow on prey availability. Intermittent sites with high water tables function like perennial sites when surface water is present; thus, management activities that promote extended periods of surface flow will provide longer temporal windows of access to critical river and riparian foraging habitats for bats.

Bat activity significantly declined throughout the dry season but bats only tracked insect availability at perennial sites and not at intermittent sites. This can be explained by variation in insect availability throughout this same time period. Specifically, shifts in insect composition may have limited bats from tracking insects along intermittent reaches. Aquatic insect abundance was relatively high at intermittent sites in May but declined significantly by June. However, terrestrial insects were fairly scarce at intermittent sites in May but increased by June. Aerial aquatic insect abundance along the San Pedro River is highest between March and May and is depressed for the remainder of the year (Chapter 4). Thus, the ratio of aquatic to terrestrial insect availability changes seasonally along the San Pedro River. Such seasonal variations also characterized forest streams in mesic regions, owing to seasonal changes in canopy cover, stream insolation, and periphyton abundance (Nakano and Murakami 2001). In these streams, peak aquatic insect availability occurred in the spring, while terrestrial insects dominated during the summer (Nakano and Murakami 2001). Not surprisingly, bat activity was significantly depressed by the experimental reduction of aquatic insects in the spring but not during the summer (Fukui et al. 2006). Unlike the mesic systems, aquatic insect emergence in arid and semiarid rivers receiving ample sunlight throughout the year is more strongly driven by the timing of seasonal floods and surface-water presence (Lytle 2002). Peak aquatic insect emergence from the San Pedro River occurs March – April, prior to the late-summer monsoon season, and is largely composed of Diptera species (Chapter 4). The timing of emergence is consistent with desert streams that experience a strong summer monsoon. For example, the majority of aquatic caddisfly emergence (86%) tends to occur prior to the long-term mean date of the first seasonal flood in Chihuahuan Desert streams (Lytle 2002) . Thus, along intermittent reaches of the San Pedro River, aquatic insect availability drives patterns in bat activity when surface flows are present, but terrestrial insect availability becomes more important as surface flows disappear.

In the current study, bat activity was related to aquatic and total insect biomass, and terrestrial and total insect abundance (Table 6). This pattern is largely driven by high-FM bat activity, which made up 48% of all recorded calls. High-FM bat activity tracked terrestrial insect abundance along perennial reaches (Table 6), and foraging activity declined substantially in response to river drying (Fig. 9a). High-FM bats, primarily composed of *Myotis* species, forage in a variety of habitats (Rogers et al. 2006) and are generally considered habitat generalists. In the current study, *Myotis velifer* made up 18% of all bats captured (Appendix D: Table 29). Previous studies have shown that this species consumes a variety of insects, including beetles, flies, moths, and true bugs (Kunz 1974, Marquardt and Choate 2009) that represented a high proportion of available insects in the current study. Low-FM bat activity also tracked both aquatic and terrestrial insect availability, suggesting that these bats are food and habitat generalists. This is corroborated by previous studies that have shown

Corynorhinus townsendii to forage along streams, canyon walls, pasture, hardwood, and pine forests (Dobkin et al. 1995, Rogers et al. 2006).

Overall, bat activity was more strongly related to insect abundance than biomass and to aquatic than terrestrial taxa. This may result from the greater number of aquatic insects than terrestrial insects collected along the San Pedro River throughout the study. Although total and ecomorphological functional-group bat activity were related to both aquatic and terrestrial insect abundance and biomass, aquatic insect abundance was the strongest predictor of low-CF bat activity in June ($R^2 = 0.51$; Table 6). Akasaka et al. (2009) found similar results with Daubenton's bat (*Myotis daubentonii*) foraging activity along a large lowland river in Japan. Previous studies utilizing fecal analysis also show aquatic insects, particularly aquatic flies, to make up a significant portion of bat diet composition (Belwood and Fenton 1976, Brigham et al. 1992, Ober and Hayes 2008b). In the current study, aquatic dipterans consistently dominated aquatic insect abundance.

Low-CF bats seemed to track terrestrial insect abundance and biomass in May but switched to aquatic insects in June. Further, these bats appeared to be unaffected by loss of surface water flow. The low-CF ecomorphological group is generally composed of larger bats that can fly longer distances (e.g., *Eptesicus fuscus*, *Tadarida brasiliensis*). Thus, localized reduction in surface flow may not affect this group, as they may simply travel to perennial reaches or intermittent reaches with surface flow. High-CF bats, which include the species *Lasiurus* *blossevillii*, accounted for less than 1% of total bat calls recorded and showed no relationship with insect availability or river drying.

Impacts of river drying on terrestrial fauna

In the current study, I found that river drying significantly affected bat activity by diminishing aerial insect availability. While the response of aquatic organisms to drying disturbances in desert rivers is well known (Stanley et al. 1994, Velasco and Millan 1998), much less is known about the response of terrestrial predators to river drying. To my knowledge, no studies have examined the response of bats to river drying. River drying may temporally result in an increase in bat activity as isolated pools along drying rivers have been shown to have higher aquatic insect densities (Canton et al. 1984, Boulton and Lake 1992, Stanley et al. 1994). For example, Extence (1981) measured increased predator abundance in response to increased insect prey density following a severe drought in a lowland English stream. On the other hand, the reduction of surface water may reduce the density of predators (Zhang et al. 1998, Lake 2003, Dewson et al. 2007). The response of predators to river drying likely depends on changes in prey availability, predator mobility, or alterations in riparian vegetation.

A previous study found significantly higher bat activity in medium and large perennial streams than small intermittent streams in a semiarid region of California, however, intermittent streams rarely flowed during the study period (Seidman and Zabel 2001). In the current study bat activity was not related to perennial or intermittent flow condition when intermittent sites were flowing. Yet, bats successfully tracked insect prey at perennial but not intermittent sites.

This suggests that bats cannot distinguish between perennial and flowing intermittent sites, but that perennial sites provide foraging conditions such that bats can successfully track insect prey, while intermittent sites do not. Perhaps isolated pools along intermittent reaches limit viable emergence and oviposition habitat for aquatic insects. Emergence rate per surface area was equivalent across perennial and intermittent sites and throughout the dry season. This is not unusual, as previous studies have shown that flow duration does not strongly correlate with emergence aquatic insect assemblage (Banks et al. 2007). However, available surface area for insects to emerge was reduced along intermittent reaches as the river dried throughout the dry season. Thus, conditions may have been such that bats were unable to track patchy prey availability along intermittent reaches but were able to successfully track insect prey along perennial reaches with continuous prey availability. Intermittent reaches along the San Pedro River still have a relatively high water table (Stromberg et al. 1996, Lite and Stromberg 2005) that supplies surface flow throughout much of the dry season. But earlier and longer-duration river drying, as is expected under continued scenarios of human appropriation, will likely further reduce suitable habitat for foraging bats.

The response of terrestrial predators to reduced or no flow conditions may be related to the mobility of the predator and the relative scale of mobility to intermittency. Fully aquatic predators (e.g., fish, Odonata nymphs) concentrated in isolated pools may exhibit increased predation rates, while more mobile emergent aquatic insect predators (e.g., dytiscid beetles and certain Hemiptera) and terrestrial predators (e.g., spiders, birds, and bats) that can move to nearby surface water sources may reduce predation risk in isolated pool habitats. Thus, more mobile predators, such as bats, may be more resistant and resilient to the effects of river drying than less mobile predators. In comparison to less mobile terrestrial predators, bats have the ability to travel long distances with relatively low energetic costs (Fenton and Rautenbach 1986, Fenton 1997). However, continued groundwater pumping and surface water declines resulting in an increase in intermittent and dry reach types, and earlier and longer duration of periods of reduced surface water flow may make it more difficult for bats to successfully cope with these conditions.

Groundwater declines and reductions in surface water flow have also been linked to changes in the riparian vegetation community. Specifically, groundwater declines have resulted in reductions in the native Fremont cottonwood-Goodding willow (*Populus fremontii* and *Salix gooddingii*) forest type (Stromberg et al. 1996), replacement of cottonwood-willow by tamarisk (*Tamarix ramosissima* and related species; Stromberg 1998), and reductions in riparian-plant species diversity (Stromberg et al. 2007). Changes in hydrologic regime and subsequent changes in riparian vegetation composition will likely affect bat foraging activity; however, few empirical studies have examined preferred bat foraging habitat, particularly in arid regions (but see Rogers et al. 2006, Williams et al. 2006). Williams et al. (2006) found significantly higher bat activity in riparian woodlands (monotypic stands of California fan palms (*Washingtonia filifera*) and mixed stands of Fremont cottonwood, velvet ash

(*Fraxinus velutina*), and Goodding willow) in comparison to riparian marsh, mesquite bosque, and riparian scrubland habitat types. This is consistent with Sherwin et al. (2000), who found that most bats preferred cottonwood forests in comparison to other riparian habitat types. Rogers et al. (2006) also found significantly higher bat activity in riparian forest and edge habitats than wetland, agricultural or restored habitats. Here, riparian forests were dominated by cottonwood (*Populus angustifolia)*, boxelder (*Acer negundo*), hawthorn (*Crataegus*), alder (*Alnus incana*), dogwood (*Cornus florida*), and willow (*Salix*) vegetation (Rogers et al. 2006). While information on ideal foraging habitat is lacking for most bat species, reductions in the cottonwood-willow forest type associated with reductions in surface water flow will likely have negative effects on bat foraging activity in the arid Southwest.

Overall, my results indicate that intermittency and river drying can lead to declines in bat activity via reductions in insect prey availability. Desert organisms are adapted to cope with naturally occurring low- and no-flow conditions. However, these adaptations have arisen on an evolutionary timescale. As such, many desert organisms will be unable to adapt to more frequent and longer duration flow reductions caused by human activities. Further, human demand for water often occurs during dry seasons, exacerbating low- and no-flow conditions. The timing of the dry season coincides with the timing of pregnancy for many bat species (Appendix D: Fig. 40; Altringham 1996). Bats have low reproductive rates compared to other mammals their size, with most species only having 1-2 young per year (Hill and Smith 1984). Therefore, increasingly frequent and longer-duration river-drying events will likely have long-term negative consequences on bat populations. Human activities continue to threaten perennial flows throughout the Southwest. Conservation of bats and many other terrestrial consumers is contingent on the maintenance of surface water flow in the San Pedro River and rivers throughout the region.

CHAPTER 4

TEMPORAL VARIABILITY IN TERRESTRIAL CONSUMER DISTRIBUTIONS ALONG TWO DESERT STREAMS WITH CONTRASTNG PATTERNS OF PREY RESOURCE SUPPLY

Abstract. Emergent aquatic insects provide significant resources for terrestrial consumers. Resource availability and tracking of aquatic insect prey by terrestrial consumers may be influenced by aquatic productivity, hydrologic regime, and riparian vegetation. To examine these relationships, I measured bat activity and insect availability along 2 streams with contrasting aquatic productivity, hydrologic regimes, and riparian vegetation. Sycamore Creek is characterized by high aquatic productivity, a hydrologic regime dominated by winter storms, and a narrow band of riparian vegetation. In contrast, the San Pedro River has low aquatic productivity, the majority of floods occur during the summer monsoon, and supports an extensive, closed-canopy gallery forest. Bat activity and insect availability were measured monthly directly above the stream and in the floodplain for one year. At Sycamore Creek, aquatic insect biomass peaked in the spring when terrestrial insect biomass was low, while terrestrial insect biomass was highest in the summer after aquatic insect biomass had declined. By contrast, aquatic and terrestrial insect availability were nearly equal or dominated by terrestrial insects throughout the spring and summer at the San Pedro River. My results suggest that the tracking of insect prey by bats varies among desert streams and this variation appears to be due to differences in insect availability in the airspace. I observed strong positive relationships between bats, emergent aquatic

insects, and terrestrial aerial insects at Sycamore Creek. At the San Pedro River, I observed weak or non-significant relationships between bats and aquatic insects, but strong relationships between bats and total (aquatic and terrestrial combined) aerial insects. The extent and diversity of riparian habitat also seems to influence relationships between bats and insect prey. Bat activity was concentrated directly above the river along Sycamore Creek, but I measured high bat activity above the river and in the floodplain at the San Pedro River. The results of this study suggest that aquatic and terrestrial prey availability is linked to stream productivity, timing of flood disturbances, and extent of riparian vegetation, and these factors can have strong effects on terrestrial food webs.

INTRODUCTION

The movement of energy, material, and organisms between rivers and riparia closely link aquatic and terrestrial ecosystems. Much research has focused on the magnitude of aquatic insect flow between aquatic and terrestrial ecosystems and its effect on the abundance (Sabo and Power 2002a), distribution (Iwata 2007), and behavior (Nakano et al. 1999b, Sabo and Power 2002b) of terrestrial consumers. Emergent aquatic insects provide an important food resource, accounting for 25-100% of the energy supply to terrestrial consumer diets (reviewed by Baxter et al. 2005). This is particularly true in desert streams, which exhibit high rates of aquatic-insect emergence (Jackson and Fisher 1986). For example, Sanzone et al. (2003) estimated that aquatic insects provided riparian spiders with almost 100% of their energy requirements along a Sonoran Desert stream during a 6 week period May – July 1997. While it is well established that aquatic insects provide a substantial portion of terrestrial consumer diet (Nakano and Murakami 2001, Collier et al. 2002), these studies have been short in duration and often do not consider temporal variability in aquatic insect availability or the effects of temporal variability on terrestrial consumers.

Aquatic insect emergence is temporally variable (Corbet 1964, Kawaguchi and Nakano 2001) and fluxes of aquatic resources from streams to land can vary considerably over time. As a result, consumer tracking of aquatic resources may depend on the timing of aquatic insect emergence. Further, resource tracking may vary across streams and may not be perfect where variability in aquatic resources is high. For example, bats successfully tracked aquatic insects at perennial sites but not intermittent sites where aquatic insect availability was more variable along a desert stream in Arizona (Chapter 3).

In temperate streams, aquatic insect emergence is seasonal, peaking in early summer prior to leaf-out and generally only lasting a few days to a few months (Sweeney and Vannote 1982). Emergence from desert streams in the southwestern United States is quite variable as well, and closely tied to the timing of floods (Lytle 2002). In desert streams with a weak summer monsoon, aquatic insect emergence is fairly continuous throughout the summer months (Jackson and Fisher 1986). However, in desert streams with a strong summer monsoon, peak emergence tends to occur earlier, prior to monsoon floods (Lytle 2002).

Previous studies showing strong effects of aquatic insects on terrestrial consumers have been generally conducted during peak aquatic insect emergence

(Sabo and Power 2002a, b). Nakano and Murakami (2001) found that aquatic insects made up the largest proportion of riparian bird diet (50-90%) November through May after riparian trees had dropped their leaves and terrestrial insects were unavailable. However, during leaf-out periods, when terrestrial insect biomass was high but aquatic insect biomass was low, birds switched their foraging efforts to terrestrial insects. Thus, temporal variability in aquatic insect availability may influence how well terrestrial consumers can track aquatic resources.

Desert river-riparian systems exhibit a wide range of forest physiognomies, ranging from open ephemeral or intermittent channels bordered by occasional woody shrubs and little canopy cover by trees to perennial rivers bordered by phreatophytic trees and full canopy closure by gallery forests. Reduced riparian habitat, high aquatic productivity, warm water temperatures, intermittent flows, and flash floods characterize many desert streams, especially those with few or no trees. These conditions contribute to high rates of secondary production (Fisher and Gray 1983, Jackson and Fisher 1986), and high emergence rates of aquatic insects (Jackson and Fisher 1986), short life cycles (Gray 1981), and rapid recovery to flood disturbance (Fisher et al. 1982). On the other hand, some Sonoran Desert streams support extensive closed gallery forests (Webb and Leake 2006), which contribute to heavy shading by riparian vegetation, cool water temperatures, and relatively low productivity. These conditions may translate into reduced aquatic insect emergence, and differences in the timing of emergence and availability of aquatic insects to terrestrial consumers.

Desert streams also exhibit large variation in hydrologic regimes. Desert hydrographs typically feature countervailing floods and dry periods, where floods and droughts may occur during a narrow or wide window of time that may or may not coincide with the peak growing season for aquatic insects (i.e., warm summer months when water temperatures promote fast larval growth; Sponseller et al. 2010). For example, some desert streams are characterized by flash floods that can occur any time throughout the year. In other desert streams, floods are highly predictable and seasonal (Sabo and Post 2008). Some desert streams are characterized by both elements of both hydrologic regimes. Hydrologic regime, extent of gallery forest, and stream productivity may affect coupling between aquatic and terrestrial food webs in desert systems. In open streams with little gallery forest, aquatic export may predominate, whereas in streams with closed gallery forests, terrestrial production is more substantial and may overwhelm aquatic export, especially if floods limit the period of growth for aquatic secondary production.

Previous studies have shown that terrestrial arthropods are affected by alterations to hydrologic regime (i.e., flow regulation, channelization; Laeser et al. 2005, Paetzold et al. 2008). Along desert rivers, intermittency and river drying can result in alterations to terrestrial arthropod community composition, richness, abundance, and biomass (Chapter 3, McCluney 2010). Variation in hydrologic regime will likely affect terrestrial consumers at higher trophic levels as well. Bats are an abundant and speciose group of terrestrial consumers in desert stream-riparian ecosystems (Rogers et al. 2006, Williams et al. 2006) that depend on aquatic insects as a food resource (Belwood and Fenton 1976, Brigham et al. 1992). Bats in the Sonoran Desert generally exhibit peak activity during warm summer months, coinciding with reproduction (May – August), and low activity the remainder of the year (September - April; Kuenzi and Morrison 2003). Bat activity has also been shown to vary in response to season (Kuenzi and Morrison 2003), fire (Malison and Baxter 2010), river drying (Chapter 3), and variation in prey resources (Chapter 5, Fukui et al. 2006, Akasaka et al. 2009). Previous studies suggest that temporal variation in bat activity may be in response to changes in aquatic insect emergence patterns (Black 1974, Fukui et al. 2006). Specifically, variation in aquatic insect life history characteristics, including timing of peak emergence, duration of emergence, and adult body size, may influence resource tracking of aquatic insect prey by foraging bats.

I set out to document temporal variation in insect availability and bat activity along 2 Sonoran Desert streams that span the variety of stream-riparian systems present in the Sonoran Desert. My goal was to quantify temporal variability in spatial patterns of aquatic and terrestrial resource tracking by bats in 2 streams with contrasting temporal patterns of aquatic and terrestrial resource supply (production, emergence, and local biomass). First, I describe temporal patterns in insect availability by measuring aquatic insect emergence, standing stocks of aquatic and terrestrial aerial insects (abundance and biomass), and standing stocks of benthic aquatic insects. Second, I compare the body size of 3 abundant aquatic insect taxa. Third, I measure temporal patterns in bat activity to explore whether bats track aquatic and terrestrial prey differently in streams with contrasting patterns of insect prey availability.

METHODS

Study sites

I conducted this study along 2 Sonoran Desert streams in Arizona, USA: Sycamore Creek and the San Pedro River from February 2008 to January 2009 (Fig. 10). I selected these streams because they vary considerably with high versus low aquatic primary productivity, hydrologic regimes dominated by winter and summer rains, and low versus high coverage by riparian vegetation, respectively.

Sycamore Creek is an intermittent stream characterized by coarse sand and gravel substrate. Sycamore Creek study sites were between 1024 – 1036 m elevation and were located in the Tonto National Forest. Sycamore Creek hydrologic regime was characterized using long-term (1960-2009) discharge data from a U.S. Geologic Survey (USGS) gaging station (0951022, Sycamore Creek near For McDowell, AZ). The watershed area at the gage was 425 km^2. Sycamore Creek is characterized by low and intermittent flows during the summer months and high and continuous flows in the winter. The majority of floods occur December – April with small flash floods occurring July – November (Fig. 11). Mean air temperature near the river was 15.5˚C during the study period (Table 7). Stream width varied from 0-20 m and sections of the stream dried in July and August. Sycamore Creek supports a narrow band of riparian trees (< 25 m from the river), primarily composed of Gooding willow

(*Salix goodingii*), ash (*Fraxinus pennsylvanica velutina*), sycamore (*Platanus wrightii*), and mesquite (*Prosopis* sp.). Limited gallery forest contributed to low shading and high streambed insolation. In addition to the gallery forest, riparian habitat included a small amount of grassland habitat nested between the gallery forest and upland desert scrub.

Sites along the San Pedro River were located in the San Pedro River Preserve; a preserve owned by The Nature Conservancy in Dudleyville, Arizona, USA. Like Sycamore Creek, the San Pedro River is an intermittent stream with coarse sand and gravel substrate. Study site elevation ranged between 603 – 610 m. Long-term discharge data from USGS gages 09471000 (San Pedro River at Charleston, AZ) and 09473000 (Aravaipa Creek near Mammoth, AZ) were used to characterize the San Pedro River hydrologic regime. Discharge measured at the San Pedro River at Charleston, AZ reflects flow conditions in the winter and dry season (October – June), while Aravipa Creek discharge is more indicative of local monsoon conditions. The watershed area for the study sites is approximately 8019 km^2. The San Pedro River is characterized by low to moderate consistent flows during the winter wet season (December – March), low and intermittent flows during the late spring and early summer dry season (April – June), and high and variable flows during the summer monsoon (July – September; Fig. 11; Hirschboeck 2009). Stream width varied from 0-15 m and sections of the river were dry in June and July. Mean air temperature near the river channel was 17.9°C during the study period (Table 7). The San Pedro River supports an extensive closed canopy gallery forest, composed of Fremont cottonwood (*Populus fremontii*), Goodding willow, and tamarisk (*Tamarix* sp.) trees. This riparian forest contributes to extensive shading and low insolation to the streambed. Riparian habitat is extensive along the San Pedro River consisting of grasslands and abandoned agricultural fields that have transitioned into grassland habitat. The floodplain was nested between gallery forest along the main channel and a band of riparian trees along a secondary channel that only flows following large precipitation events.

I selected 3 sites along each stream. Sites were 50-m long and located ~500 m stream distances from each other. Sites consisted of sampling locations in the stream and in the floodplain (25-m from the stream edge in grassland habitat). I measured productivity 3 times throughout the year at the 3 sites in both streams. I measured prey resource availability, bat acoustic activity, and temperature monthly at the 3 sites located along both streams. Bats were captured monthly at 1 site along each stream. Aerial insect availability, bat acoustic activity, and bat capture rate were measured directly above the stream and in the floodplain. Bat acoustic activity and capture rate were measured concurrently with insect availability each month.

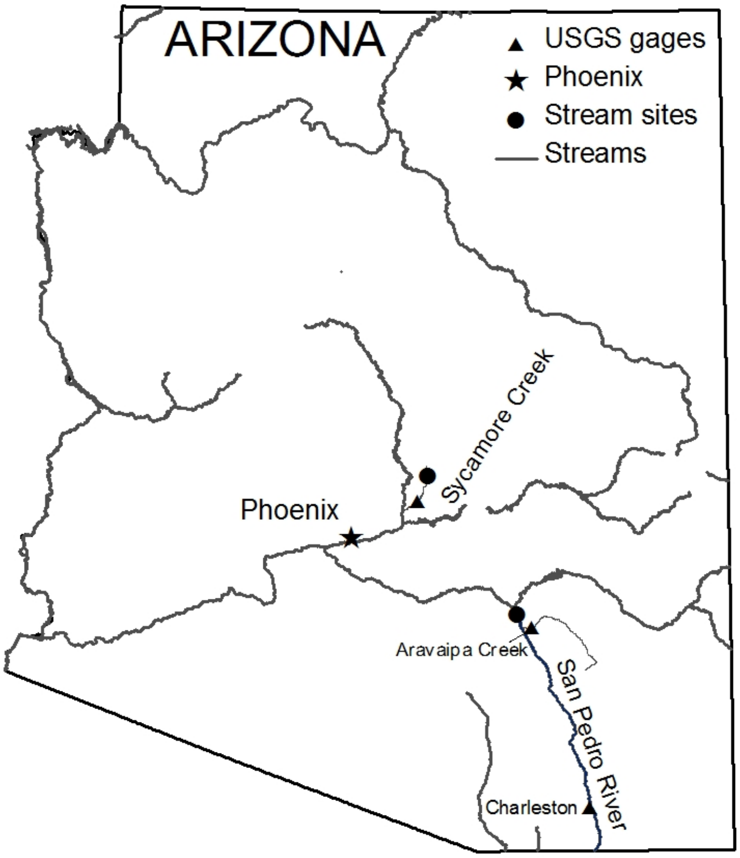

FIG. 10. Map showing study site and USGS gage site locations.

TABLE 7. Biological and physical parameters in Sycamore Creek and San Pedro River during the study period.

Parameter	Sycamore Creek					San Pedro River				
	Mean	SE	Min	Max	N	Mean	SE	Min	Max	N
Aquatic insect emergence (mg m^{-2} day^{-1})	171.3	64.8	0.2	553.1	12	24.3	8.0	0.0	87.6	12
Aquatic aerial insect biomass above river (mg/trap)	343.8	173.9	2.9	2124.4	12	164.5	49.5	32.8	475.5	11
Aquatic aerial insect biomass in floodplain (mg/trap)	85.0	44.4	1.7	559.0	12	2.6	0.9	0.3	11.0	12
Terrestrial aerial insect biomass above river (mg/trap)	123.9	36.2	0.0	311.4	12	194.4	54.8	0.0	507.0	11
Terrestrial aerial insect biomass in floodplain (mg/trap)	106.9	35.0	0.0	376.4	12	9.6	2.4	0.3	25.4	12
Total aerial insect biomass above river (mg/trap)	467.7	174.1	2.9	2167.0	12	358.8	75.1	35.8	738.9	11
Total aerial insect biomass in floodplain (mg/trap)	191.9	55.7	1.7	623.1	12	12.2	2.9	1.0	32.0	12
Benthic insect biomass (mg/trap)	51.8	24.7	0.6	271.6	12	19.7	5.5	0.0	64.4	12
Bat acoustic activity above river (min/night)	13.1	7.2	0.0	87.7	12	37.9	17.2	0.2	159.0	11
Bat acoustic activity in floodplain (min/night)	7.6	2.9	0.0	34.2	12	29.4	13.3	0.6	128.0	11
Water temperature (°C)	15.5	1.2	10.0	21.5	12	18.2	1.5	10.0	24.6	12
Air temperature above river (°C)	15.5	2.1	5.2	25.4	12	17.9	2.5	5.4	29.9	12
Air temperature in floodplain (°C)	15.4	2.4	4.0	27.1	12	17.9	2.6	5.1	30.8	12
Discharge (m^3/s)	0.7	0.1	0.0	42.5	366	1.0	0.1	0.0	30.9	366
Wetted width (m)	5.9	1.0	2.6	11.5	12	4.3	0.6	0.7	7.4	12

Notes: Monsoon flooding prevented aerial insect abundance and biomass data from being collected in August along the San Pedro River. Cicada noise prevented bat acoustic activity monitoring in July along the San Pedro River. Discharge data summarized from mean daily values during study period. Minimum wetted width is not 0 m because the streams did not dry completely at all 3 sites during the study period. SE is standard error; Min is minimum; Max is maximum; N is number of months sampled.

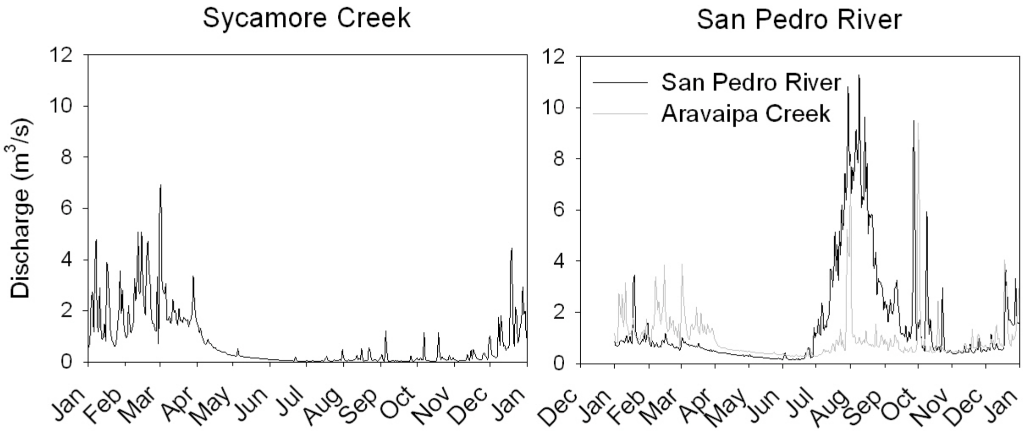

FIG. 11. Mean daily discharge in Sycamore Creek and San Pedro River. Sycamore Creek discharge from 1960 – 2009 (data from USGS NWISweb gage 09510200, Sycamore Creek near Fort McDowell, AZ). San Pedro River discharge from 1904 – 2009 (09471000, San Pedro River at Charleston, AZ) and Aravaipa Creek discharge from 1931-2009 (09473000, Aravaipa Creek near Mammoth, AZ).

Comparative climate and hydrology

At each stream, I measured water temperature, air temperature above the river, and air temperature in the floodplain for 4 days each month concurrent with insect sampling using Tidbit data loggers (http://www.onsetcomp.com) at 3 sites along both streams. Air temperature was measured ~1 m off the ground using Tidbits shaded by vegetation but not enclosed by radiation shields. Mean daily discharge data was obtained from the USGS NWIS (National Water Information System web database (http://waterdata.usgs.gov/nwis/sw) using the gages described above. Wetted width was measured at 3 locations at each site in both streams each month.

Stream productivity

I measured chlorophyll *a* concentration and periphyton biomass as a proxy for stream productivity in May, September, and January at the 3 sites in each study stream. Replicate (3) rocks were randomly selected from each site during dry season (May), monsoon (September), and winter (January). Rocks were scrubbed, rinsed with DI water, separated into equal volumes, and filtered onto 2 GF/F filters. Filters used to determine periphyton biomass were weighed, combusted at 500˚C for 1 hour, and reweighed. Filters used to determine chlorophyll *a* concentration were frozen, and chlorophyll *a* was then extracted by soaking in 10-mL methanol. Chlorophyl *a* was measured using a fluorometric method and acidified to correct for any pheophytin (American Public Health Association 1995).

Prey resource availability

I measured prey resource availability monthly at each site in both streams 3 different ways: 1) aquatic insect emergence, 2) aquatic and terrestrial aerial insect abundance and biomass, and 3) benthic aquatic insect abundance and biomass. I measured the timing and duration of aquatic insect emergence monthly using 3 replicate 0.25-m^2 floating emergence traps at each site. Emergence traps were deployed for 4 days each month. After 4 days, I collected insects from each emergence trap, preserved them in ethanol until they were processed in the lab. Monthly variability in aquatic and terrestrial aerial-insect abundance and biomass (hereafter standing stocks) were measured using 3 replicate sticky traps set at each site. Sticky traps were attached to 1.8-m bamboo gardening poles set in the stream and floodplain (25-m from the stream edge) and deployed for 4 days each month. Sticky traps consisted of projector sheets (603.2-cm^2) coated with Tangle-Trap adhesive (Tanglefoot, Grand Rapids, Michigan, USA). After 4 days, sticky traps were collected, covered with cellophane, and returned to the lab to be processed. Additionally, 3 replicate Surber samples (961-cm^2, 1-mm mesh) were collected from each site in each stream monthly to estimate the timing and duration of juvenile benthic insect life-history stage. Surber samples were collected from similar substratum (sand to coarse gravel) in riffle habitat at each site. Collected benthic samples were stored on ice until returned to the lab. Upon return to the lab, organisms were sorted and preserved in ethanol until indentified.

I subsampled aerial insects using a 2.54 cm X 2.54 cm grid. All insects were identified in 10 randomly selected squares; insects were identified to order, except for Diptera and Coleoptera, which were identified to family. Aerial insects were categorized as aquatic or terrestrial. Insects were considered terrestrially derived only if they were the product of terrestrial secondary production (i.e., flying adult aquatic insects were categorized as aquatic insects). Aquatic and terrestrial insect abundance was recorded for the 10 squares and multiplied by 9.35 to estimate insect abundance for the entire sticky trap. Emergent aquatic insects and benthic insects were identified to family and genera when possible. Insects were identified using Borror et al. (1989) and Merritt et al. (2008). I measured the length (±1 mm) of subsampled aerial insects and all emergent and benthic insects using a Leica S6D dissecting microscope. I then determined insect biomass using established length-mass regressions (Benke et al. 1999, Sabo et al. 2002). I report results for abundance in the appendix only (Appendix E: Table 30).

Terrestrial consumer distribution

Bat foraging activity was measured monthly at each stream both acoustically and with mist nets. Bat activity was measured acoustically using 4 – 6 Anabat II bat detectors (Titley Electronics, Ballina Australia) connected to zero-crossings analysis interface modules (Anabat CF Storage ZCAIM). From February – July, bat activity was measured monthly at each site along both streams. At each site, bat activity was measured above the river and in the floodplain (25-m from the river edge). Two bat detectors were lost during a monsoon flood in July. Therefore, for the August – January sampling period, bat acoustic activity was only measured a 2 sites along each study stream each month. Bat activity was recorded at each stream from dusk until dawn, for 1 night each month. To maximize detection, bat detectors were set in areas with no vegetation obstruction.

Due to similarity in bat calls among different species (Thomas 1988, Krusic et al 1996), I did not identify bats to species by their calls. However, I did assign bat calls to ecomorphological functional groups – groups of bats with similar call structure that tend to be associated with similar habitat use and food resource partitioning (Aldridge and Rautenbach 1987, Saunders and Barclay 1992). Ecomorphological groups include high frequency modulated (FM), low FM, high constant frequency (CF), and low constant frequency. High-FM calls had a minimum frequency > 35 kHz and a call duration < 6 ms, while low-FM calls had a minimum frequency < 35 kHz and a call duration < 6 ms. High-CF calls had a minimum frequency > 35 kHz and a call duration > 6 ms and low-CF calls had a minimum frequency < 35 kHz and a call duration > 6 ms. FM calls are characterized by varying frequency and tend to be emitted by bats foraging in cluttered environments with dense vegetation, while CF calls tend to be produced by bats foraging in open environments (Schnitzler and Kalko 2001). I report results of acoustic activity of all bats combined below and results from ecomorphological groups in Appendix E only. I report average bat activity measured by detectors set at 2-3 sites above the river and in the floodplain to generate a monthly average for each habitat type.

At 1 site each month, I captured bats using four 38-mm mesh nylon mist nets (2.6-m X 9-m): 2 nets set above the stream and 2 in the floodplain to determine species presence along each stream. Mist nets were left open for 4 hours after sunset during each sampling event. Mist netting did not occur during precipitation events or when temperatures dropped below 10˚C. Upon capture, species, gender, and reproductive status were recorded. Captured bats were marked by cutting hair from the dorsal side to identify individuals recaptured on the same night. I used the same mist-netting locations each month but allowed at least 20 days to pass before mist netting at the same location. I did not acoustically monitor or capture bats on the 2 nights prior to or after the full moon to reduce sampling effects caused by bat avoidance of mist nets due to better visibility.

Statistical Analysis

Differences in chlorophyll *a* and periphyton biomass among season were analyzed using repeated measures analysis of variance (RM ANOVA) followed by a Holm-Sidak's post hoc multiple comparison tests. Assumptions of RM ANOVA were met (e.g., normality, equal variance, compound symmetry). Differences in insect body length between the two study streams were assessed using a t-test using mean monthly values from the 3 study sites at each stream. I used Pearson product-moment correlation and linear regression analysis to examine relationships between bat activity and insect availability and physical parameters measured. Here I used monthly mean values from each study site.

RESULTS

Comparative climate & hydrology

Water and air temperature followed expected seasonal patterns. Water temperature peaked at 21.5˚C in August in Sycamore Creek and peaked at 24.6˚C in the San Pedro River (Table 7). Air temperature was similar at the river and in the floodplain at both streams. Air temperature peaked in June at Sycamore Creek (27.1˚C) and in July at the San Pedro River (30.8˚C). Sycamore Creek discharge peaked in December at 42.5 m^3/s with a few small floods February, September, and November (Fig. 12). In contrast, discharge was elevated July through October but depressed the remainder of the year in the San Pedro River (Fig. 12). Mean wetted width was 5.9 m at Sycamore Creek and 4.3 m at the San Pedro River.

Stream productivity

Chlorophyll *a* concentration and periphyton biomass did not vary significantly among season in Sycamore Creek. Chlorophyll *a* concentration was significantly higher in the winter than during the monsoon, while periphyton biomass was significantly higher during the dry season than the monsoon or winter in the San Pedro River (Table 8). RM ANOVA tables are reported in Appendix E: Table 31.

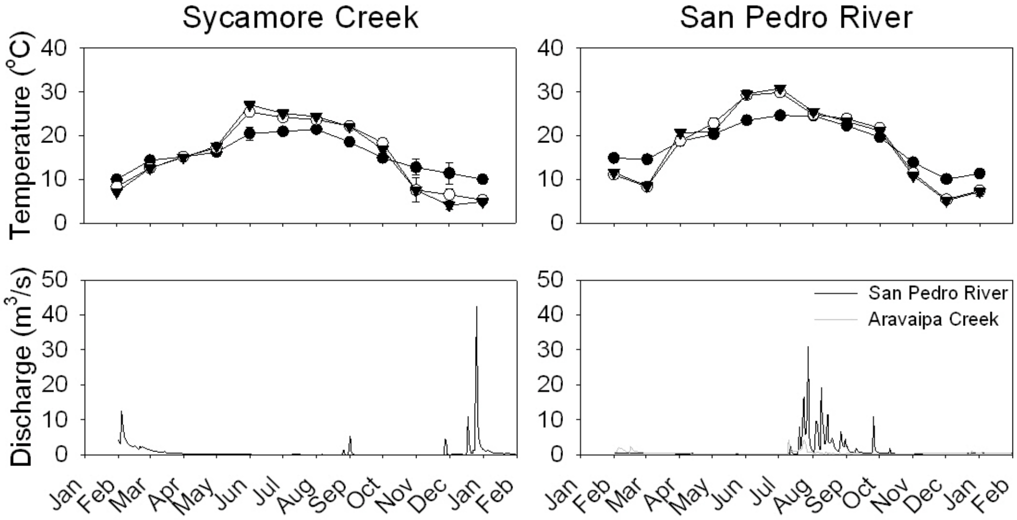

FIG. 12. Temporal variation stream water temperature, air temperature, and discharge in Sycamore Creek and San Pedro River. Temperature data are mean (± SE) values from monthly sampling conducted February 2008 – January 2009. Filled circle represent water temperature, open circles represent air temperature at the rivers edge, and filled triangles represent floodplain air temperature. Discharge data are mean daily values during study period.

TABLE 8. Mean (± SE) chlorophyll *a* and periphyton biomass from rocks at each study site.

Parameter	Dry season	Monsoon	Winter	*P*
Sycamore Creek				
Chlorophyll *a* (mg/m^2)	409.6 (195.7)	59.8 (7.7)	6.5 (5.8)	0.115
Periphyton biomass (g/m^2)	15.4 (4.3)	9.3 (0.6)	0.7 (0.1)	0.054
San Pedro River				
Chlorophyll *a* (mg/m^2)	70.5 (11.0) AB	2.1 (0.4) B	95.0 (30.2) A	0.036
Periphyton biomass (g/m^2)	17.5 (5.8) A	1.3 (0.2) B	5.8 (0.7) B	0.02

Notes: Data are from dry season (May), monsoon (September), and winter (January) sampling periods. Different letters indicate significant differences between sampling periods (RM ANOVA, $P < 0.05$).

Prey resource availability

Aquatic insect emergence in Sycamore Creek was highest March through June with peak emergence occurring in May (843.9 individuals m^{-2} d^{-1} and 553.1 mg m^{-2} d^{-1}, Table 7, Fig. 13). Total emergence from Sycamore Creek throughout the study period was 73,265 individuals m^{-2} y^{-1} and 63.1 g m^{-2} y^{-1}. Mean emergent aquatic insect abundance and biomass was 4-7 fold higher in Sycamore Creek than in the San Pedro River with peak emergence occurring in March (165.7 individuals m^{-2} d^{-1} and 87.6 mg m^{-2} d^{-1}; Table 7, Fig. 13). Total emergence from the San Pedro River during the study period was 16833 individuals m^{-2} y^{-1} and 9.0 g m^{-2} y^{-1}. Chironomidae body lengths were significantly larger from Sycamore Creek than the San Pedro River (*t*-test, $t = -3.504$, $df = 120$, $P < 0.001$; Fig. 14). Annual mean Chironomidae body length was 2.7 mm and 2.0 mm in Sycamore Creek and the San Pedro River, respectively (Appendix E: Table 32).

Chaoboridae and Baetidae body lengths did not differ significantly between the two study streams. Annual mean Chaoboridae length was 2.6 mm in Sycamore Creek and 2.3 mm in the San Pedro River. Annual mean Baetidae length was 5.7 mm in Sycamore Creek and 4.2 mm in San Pedro River (Appendix E: Table 32).

Standing stocks of aquatic and total aerial insects peaked in April above the river and in the floodplain at Sycamore Creek (Fig. 13; Appendix E: Fig. 41). Standing stocks of terrestrial aerial insects were highest April, but sustained through September along Sycamore Creek and were similar above the river and in the floodplain (Fig. 13; Appendix E: Fig 41). Standing stocks of aquatic aerial insects were substantially lower along the San Pedro River than Sycamore Creek. At the San Pedro River, aquatic aerial insect abundance and biomass were highest March – May and depressed the remainder of the year. By contrast, standing stocks of terrestrial aerial insects were higher along the San Pedro River than Sycamore Creek. Terrestrial aerial insects exhibited peak standing stocks above the river in June and October (Fig. 13).

Benthic insects in Sycamore Creek followed a similar pattern as insect emergence rates, peak abundance and biomass occurring in May (Fig. 13). In the San Pedro River, benthic-insect standing stocks were consistently lower than Sycamore Creek with peak abundance and biomass occurring in May and a second peak in December (Fig. 13).

The proportion of aquatic and terrestrial insect availability varied throughout the year at the 2 study streams. In Sycamore Creek, aquatic insects made up the majority of aerial insect biomass February – May (76.3 – 98.0%), while terrestrial insects dominated July – September (66.8 – 83.0%). At the San Pedro River, aside from peak emergence in March, aquatic and terrestrial insect availability were nearly equal or dominated by terrestrial insects. Terrestrial insects made up 35.7 – 47.0% of aerial insect biomass February – May and 72.5 – 86.5% June – October.

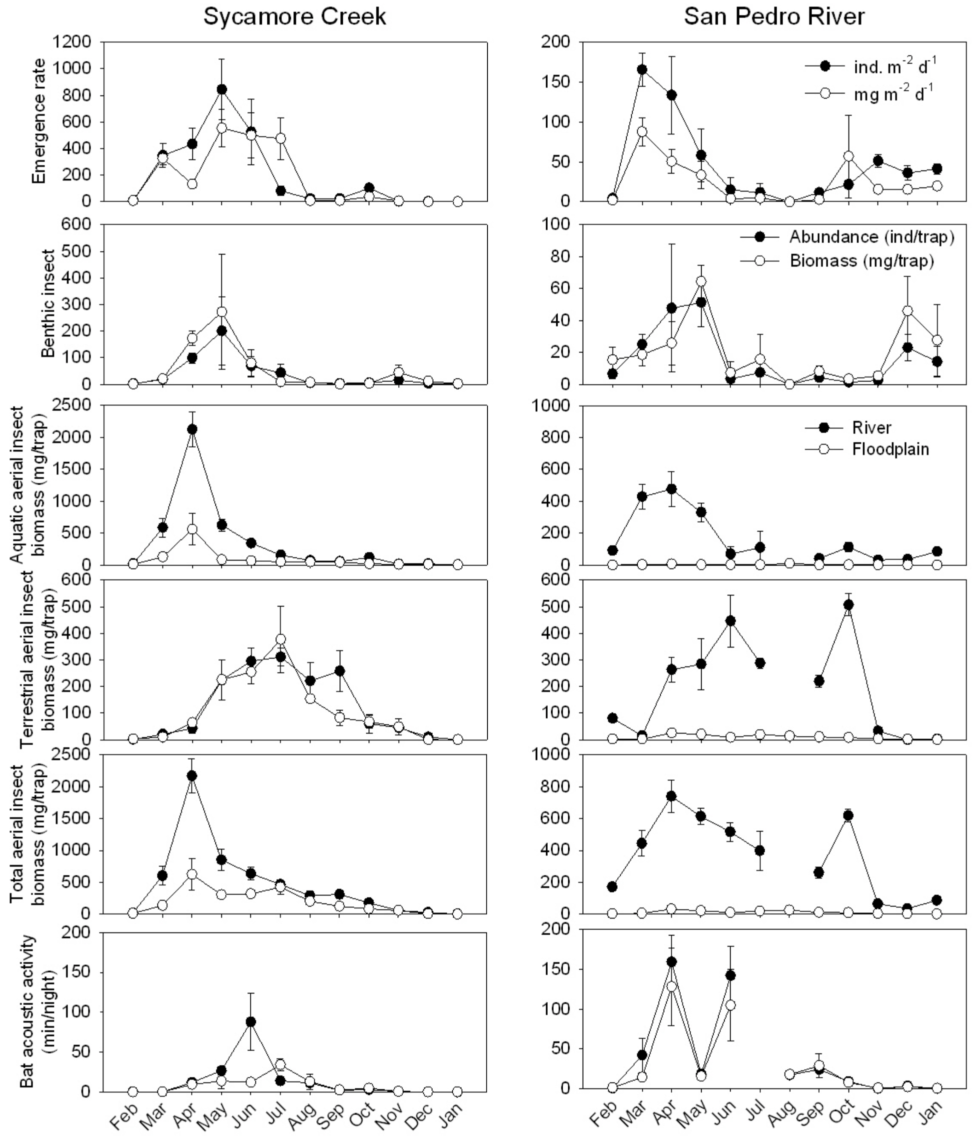

FIG. 13. Temporal variation of aquatic insect emergence rate; aquatic, terrestrial, total aerial insect abundance and biomass; and benthic insect abundance and biomass in Sycamore Creek and San Pedro River. Data are mean (± SE) values from monthly sampling conducted February 2008 – January 2009. For aerial insects, filled circles denote samples collected above the stream and open circles denote samples collected 25-m from the stream in the floodplain. Note different scales for Sycamore Creek and the San Pedro River.

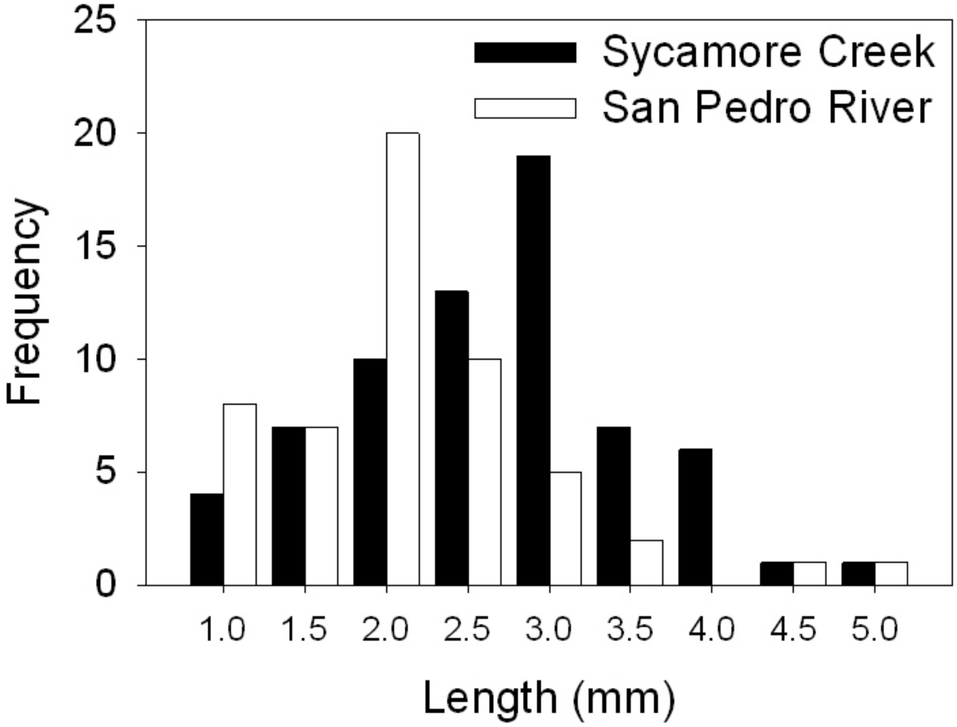

FIG. 14. Chironomidae body length distribution from Sycamore Creek and the San Pedro River.

Bat activity

Sycamore Creek and the San Pedro River had similar bat species richness (8 species) and abundance (35 and 40 bats captured, respectively; Table 9). Total annual bat activity was higher along the San Pedro River (mean ± SE: 37.9 ± 17.2 min/night) than Sycamore Creek (mean ± SE: 13.1 ± 7.2 min/night; Table 7). Temporal patterns in bat activity varied between the two streams as well. Along Sycamore Creek, bat acoustic activity peaked in June above the river (87.7 min/night) and in July above the floodplain (34.2 min/night; Fig. 13). On the other hand, at the San Pedro River bat activity was highest in April and June above the river (159.0 and 141.9 min/night, respectively) and in the floodplain (128.0 and 104.7 min/night, respectively; Fig. 13). Bat capture data followed a similar pattern with peak capture rates in June and July at Sycamore Creek and April at the San Pedro River (Appendix E: Tables 33 and 34).

The majority of bats recorded at both streams were high-FM bats (50.3 and 50.5% at Sycamore Creek and the San Pedro River, respectively). Low-FM bats and low-CF bats also made up a large proportion of bat calls recorded at Sycamore Creek (15.6 and 14.9%, respectively). At the San Pedro River, low-FM bats made up 8.2% of bat calls and low-CF bats made up 2.3% of bat calls. High-CF bats were only identified at Sycamore Creek in April.

Regression analysis showed that relationships between bat activity and insect prey varied between study streams. At Sycamore Creek, bat activity increased with aquatic insect emergence (linear regression, $F = 24.2$, $df = 28$, $P < 0.001$) and benthic-insect standing stocks (linear regression, $F = 12.6$, $df = 28$, $P = 0.001$; Fig. 15). However, bat activity was not related to aquatic insect emergence or benthic-insect standing stocks at the San Pedro River (Fig. 15; Appendix E: Fig. 42). Bat activity was positively related to aquatic, terrestrial, and total aerial insect standing stocks above the river and in the floodplain at Sycamore Creek (Fig. 16; Appendix E: Fig. 43). Here, bats tracked aerial insects similarly above the river and in the floodplain. That is, correlations between bat activity and biomass of aquatic aerial insects above the river and in the floodplain had similar slopes (river $b_1 = 0.47$ and floodplain $b_1 = 044$). I found similar slopes when I examined correlations between bat activity and terrestrial and total aerial insect biomass above the river and in the floodplain (terrestrial aerial insects: river b_1 = 0.53 and floodplain b_1 = 0.46; total aerial insects: river b_1 = 0.54 and floodplain b_1 = 0.54) at Sycamore Creek. Bat activity and aerial insect standing stocks were positively related above the river and in the floodplain at the San Pedro River as well (Fig. 16; Appendix E: Fig. 43). However, relationships between bat activity and standing stocks of aerial insect differed above the river than in the floodplain. Above the river, bat activity and aquatic and terrestrial aerial insect biomass were positively correlated, with slopes less than 1 (aquatic aerial insects b_1 = 0.66; terrestrial aerial insects b_1 = 0.33). In the floodplain, bat activity and aerial insect standing stocks were positively correlated with slopes greater than 1 (aquatic aerial insects b_1 = 1.57; terrestrial aerial insects b_1 = 1.06). Relationships between bat activity and total aerial insect biomass were positive, with slopes greater than 1 both above the river (b_1 = 1.06) and in the floodplain (b_1 = 1.23) at the San Pedro River. Similar relationships were seen with high and low frequency-modulated bats and low constant-frequency bats and insect prey availability at both streams (Appendix E: Figs. 44 and 45, Table 35).

At Sycamore Creek, terrestrial aerial insect biomass was the strongest predictor of bat acoustic activity above the river and in the floodplain at Sycamore Creek, followed by emergent aquatic insects, total aerial insects, aquatic aerial insects, and benthic insects (Table 10). At the San Pedro River, total aerial insect biomass was the strongest predictor of bat activity followed by aquatic and terrestrial aerial insect biomass (Table 10). Bat capture rate was positively correlated with biomass of terrestrial aerial insects (R = 0.81, P = 0.02) and aquatic-insect emergence (*R* = 0.76, *P* = 0.03) at Sycamore Creek (Table 10). However, total-standing stocks of aerial insects did not predict bat capture rate at Sycamore Creek. By contrast, at the San Pedro River, total aerial insect abundance in the floodplain was the only significant predictor of bat capture rate above the river (*R* = 0.76, *P* = 0.03; unpublished data).

TABLE 9. Bat species captured at Sycamore Creek and the San Pedro River.

		Total number captured			
		Sycamore Creek		San Pedro River	
Scientific name	Common name	Stream	Floodplain	Stream	Floodplain
Phyllostomidae					
Macrotus californicus	California leaf-nosed bat	0	0	2	3
Vespertilionidae					
Myotis auriculus	Southwestern myotis	0	0	1	0
Myotis californicus	California myotis	2	0	0	0
Myotis velifer	Cave myotis	13	0	8	0
Myotis yumanensis	Yuma myotis	8	0	8	0
Lasionycteris noctivagans	Silver-haired bat	3	0	0	0
Eptesicus fuscus	Big brown bat	5	0	2	0
Lasiurus xanthinus	Western yellow bat	0	0	3	0
Lasiurus cinereus	Hoary bat	1	0	0	0
Antrozous pallidus	Pallid bat	2	0	7	5
Corynorhinus townsendii pallescens	Pale Townsend's big-eared bat	1	0	0	0
Molossidae					
Tadarida brasiliensis	Mexican free-tailed bat	0	0	1	-
Total number captured		35	0	32	8

Notes: Bats were captured during eight 4-hr capture nights at each stream during study period (February 2008 – January 2009).

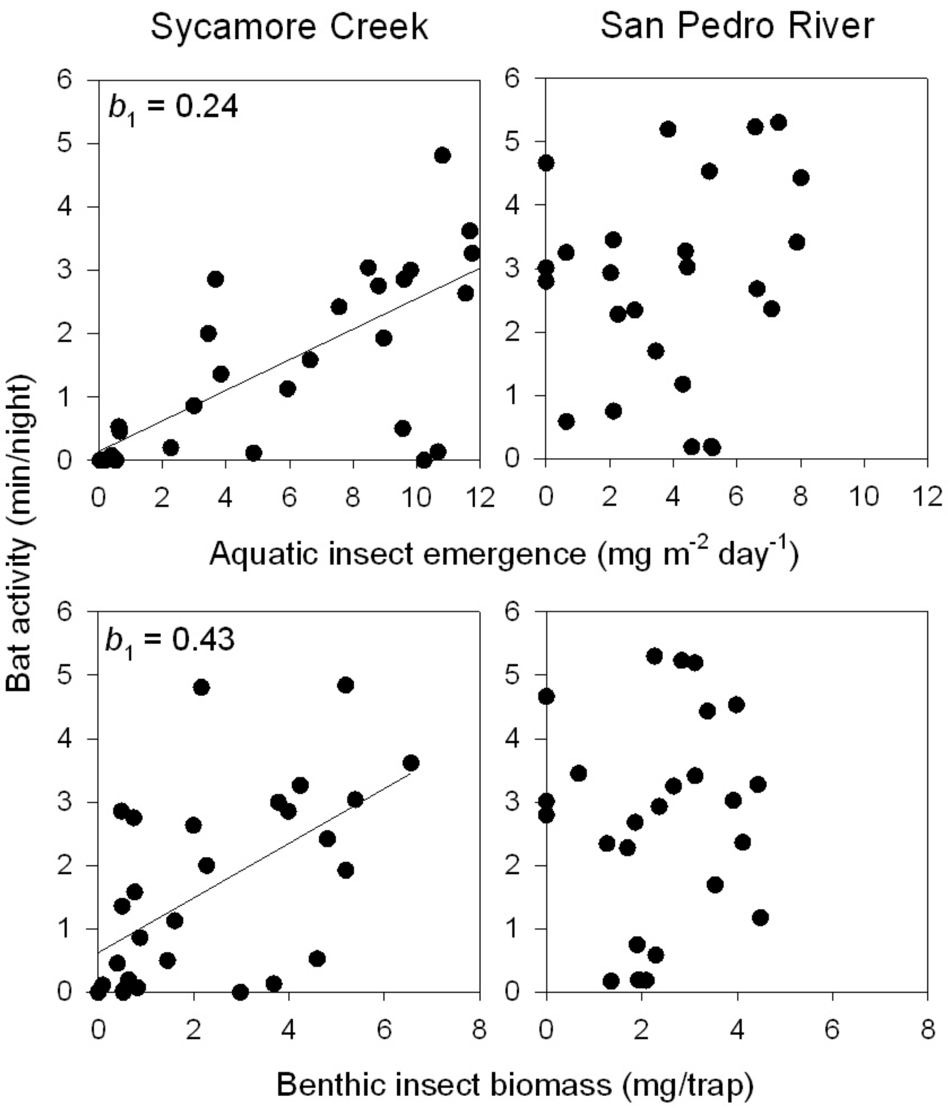

FIG. 15. Relationship between bat acoustic activity and aquatic insect emergence and benthic insect abundance at Sycamore Creek and the San Pedro River. Data are paired monthly values from each study site. Data were ln +1 transformed. b_1 = slope.

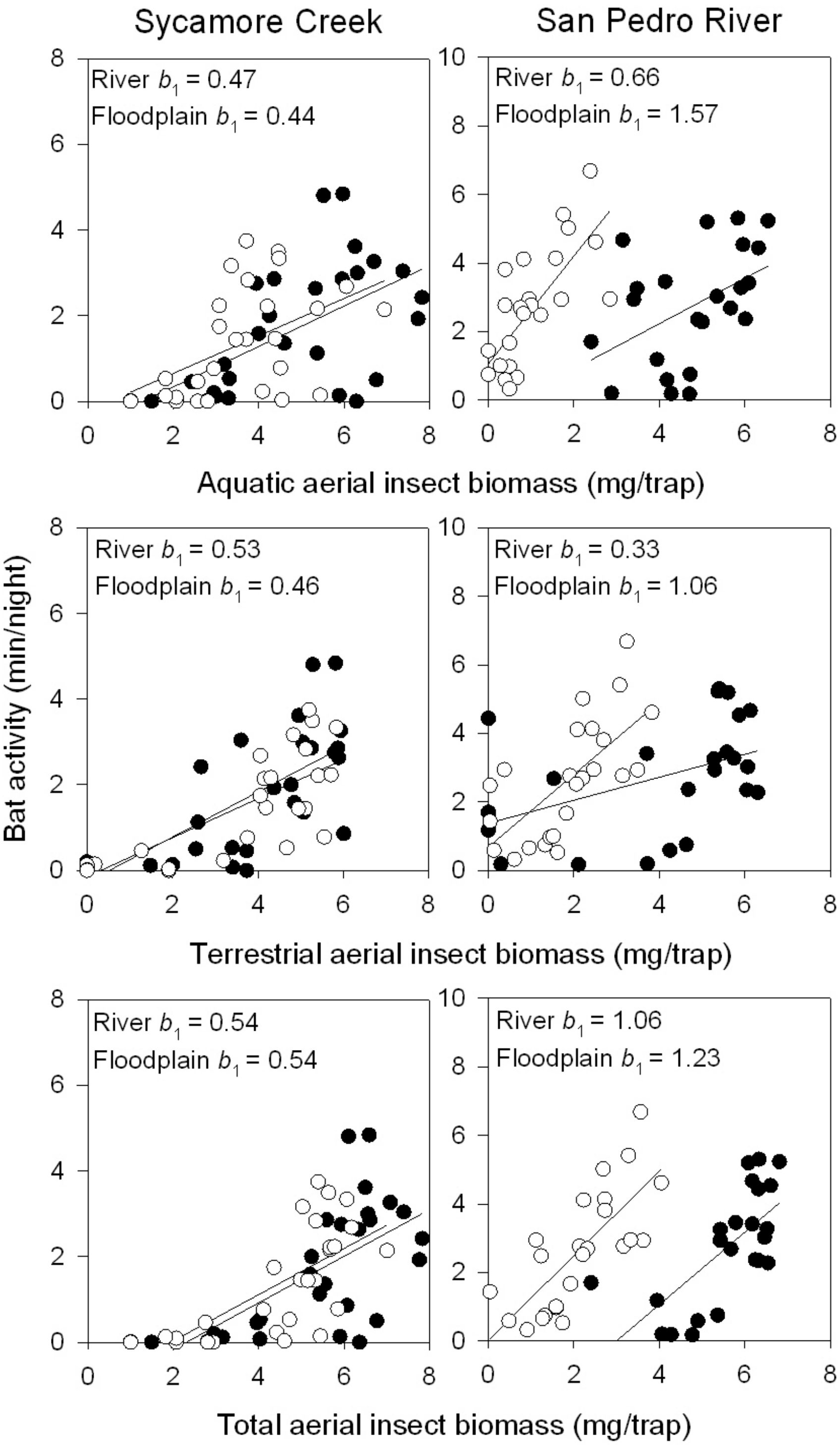

FIG. 16. Relationship between bat acoustic activity and aquatic, terrestrial, and total aerial insect biomass at Sycamore Creek and the San Pedro River. Data are paired monthly values from each study site. Filled circles denote samples collected above the stream and open circles denote samples collected 25-m from the stream in the floodplain. Data were ln +1 transformed. b_1 = slope.

TABLE 10. Pearson product-moment correlations between bats and insect prey above the stream and in the floodplain.

	Sycamore Creek		San Pedro River	
	Stream	Floodplain	Stream	Floodplain
Bat activity				
Aquatic insect emergence (mg m^{-2} day^{-1})	0.69, < 0.001	0.54, < 0.001	-	-
Aquatic aerial insect biomass (mg/trap)	0.58, < 0.01	0.50, 0.01	0.47, 0.02	0.72, < 0.01
Terrestrial aerial insect biomass (mg/trap)	0.73, < 0.01	0.79, < 0.01	0.44, 0.03	0.67, < 0.01
Total aerial insect biomass (mg/trap)	0.66, < 0.01	0.71, < 0.01	0.68, < 0.01	0.75, < 0.01
Benthic insect biomass (mg/trap)	0.57, < 0.001	-	-	-
Bat capture rate				
Aquatic insect emergence (mg m^{-2} day^{-1})	0.76, 0.03	-	-	-
Aquatic aerial insect biomass (mg/trap)	-	-	-	-
Terrestrial aerial insect biomass (mg/trap)	0.81, 0.02	-	-	-
Total aerial insect biomass (mg/trap)	-	-	-	-
Benthic insect biomass (mg/trap)	-	-	-	-

Notes: Data are monthly values from each site at Sycamore Creek and the San Pedro River. Pearson correlation coefficients and *P* values are shown for significant relationships. Data were ln +1 transformed. Dashes (-) indicate non-significant relationships.

DISCUSSION

Aquatic ecosystems have strong effects on consumers in adjacent terrestrial ecosystems by providing critical prey resources. In desert regions, aquatic ecosystems supply terrestrial consumers with aquatic insects during varying amounts of time throughout the year, and provide important habitat for terrestrial insects and longer-lived aquatic insects. In this paper, I show that 2 Sonoran Desert streams exhibit contrasting patterns of prey availability. My results further suggest that the ability of a highly mobile terrestrial consumer to track insect prey varies among desert streams and this variation may be due—at least in part—to observed differences in insect emergence and aerial insect availability in airspace. Specifically, stronger relationships between bats and aquatic insects at Sycamore Creek may be due to temporal asynchrony in aquatic and terrestrial prey availability. By contrast, weaker or non-significant relationships between bats and aquatic insects but stronger correlations between bats and total insects at the San Pedro River may be due to synchronous aquatic and terrestrial insect availability. Further, bats tracked emergent, aerial, and benthic insects at Sycamore Creek, a stream characterized by constant and high rates of aquatic insect emergence throughout the spring and summer, but bats only tracked aerial insects at the San Pedro River, a stream characterized by a punctuated emergence in the early spring. Extent of riparian gallery forest may affect interactions between terrestrial consumers and insect prey as well. In the stream with a narrow band of riparian habitat, bat activity was concentrated directly above the river. However, in the stream characterized by an ample riparian habitat consisting of a closed canopy gallery forest and extensive riparian grasslands, bat activity was similar above the river and in the floodplain. My results suggest that aquatic and terrestrial insect prey availability is tied to stream productivity, timing of flood disturbances, and extent of riparian vegetation, and these factors can have far reaching effects on terrestrial food webs.

Prey resource availability

Insect availability varied considerably throughout the study. Contrasting patterns in insect availability were likely related to differences in stream productivity, hydrologic regime, and riparian vegetation. At Sycamore Creek, aquatic insect availability was high and continuous throughout the spring and summer. By contrast, aquatic insect availability at the San Pedro River was low and concentrated to the spring (March – May). Chlorophyll *a* concentrations indicate that primary production was much higher in Sycamore Creek than the San Pedro River contributing to high rates of aquatic insect emergence and aquatic aerial and benthic insect standing stocks at Sycamore Creek. Chlorophyll *a* concentrations were similar to values previously measured at Sycamore Creek (Fisher et al. 1982, Peterson and Grimm 1992, Holmes et al. 1998). Despite warmer temperature, the closed gallery forest contributed to high canopy cover, heavy shading, and reduced primary productivity at the San Pedro River. Thus, it is not surprising that aquatic insect emergence was substantially higher from Sycamore Creek than the San Pedro River. Annual emergence from Sycamore Creek (63.1 g m^{-2} y^{-1}) was higher than emergence measured previously from this stream (23.1 g m^{-2} y^{-1}), and much higher than the San Pedro River (9.0 g m^{-2} y^{-1})

and emergence rates from various aquatic habitats in a wide variety of biomes (Jackson and Fisher 1986).

In temperate regions, temporal patterns of aquatic insect availability are often related to stream productivity. Aquatic insect availability tends to peak in the spring and decline throughout the summer, coinciding with decreases in canopy cover, stream isolation, and periphyton abundance (Nakano and Murakami 2001). However, in arid and semiarid rivers that receive ample sunlight throughout the year, the timing of seasonal floods drives aquatic insect availability. Variation in flow is closely tied to several aquatic insect characteristics including abundance (Konrad et al. 2008), oviposition (Peckarsky et al. 2000), and emergence (Whiles et al. 1999). The timing of emergence relative to seasonal flooding in desert streams is well established (Lytle 2002). In the San Pedro River, emergence had a short duration and occurred early, prior to the summer monsoon. Previous studies have shown similar patterns of aquatic insect emergence from desert streams with strong monsoon seasons (Lytle 2002). For example, a study examining aquatic insect emergence from 3 Chihuahuan Desert streams found that 86% of caddisfly emergence occurred prior to the long-term mean date of the first seasonal flood (Lytle 2002). It is not uncommon for flash floods in desert streams to displace and kill > 90% of aquatic insect standing stocks (Gray and Fisher 1981, Molles 1985, Grimm and Fisher 1989, Lytle 2000). In the current study, a July monsoon flood (peak discharge: 73.1 m^3/s) resulted in 100% mortality of juvenile aquatic insects in the San Pedro River. This flood reduced emergence to zero as well. It is critical for aquatic insects to emerge prior to monsoon floods, as insects have a higher probability of surviving as aerial adults and successfully recolonizing (Lytle 2001, Gray 1981). By contrast, emergence rate and benthic insects standing stocks were lowest in January in Sycamore Creek, coinciding with peak discharge associated with winter storms. Thus, a combination of low summer production, closed gallery forest, and a strong summer monsoon appeared to contribute to a punctuated spring emergence from the San Pedro River. On the other hand, high summer productivity, limited canopy cover, and a weak summer monsoon seemed to result in high and extended aquatic insect emergence from Sycamore Creek.

Stream productivity and hydrologic regimes may also influence the size of emergent aquatic insects. Chironomidae body lengths were significantly longer from Sycamore Creek than the San Pedro River. High algal resource availability and extended periods of time in the spring and summer without flood disturbances allowed these organisms to grow large in Sycamore Creek prior to emergence.

While aquatic insect availability was consistently higher at Sycamore Creek than the San Pedro River, terrestrial insect availability was higher along the San Pedro River and available for a longer portion of the year than along Sycamore Creek. Here the extensive gallery forest likely facilitated high terrestrial insect production throughout the spring and summer. Thus, desert streams play 2 roles for terrestrial consumers. First, they provide aquatic insects that subsidize terrestrial consumers during critical times of the year. This is more pronounced in the stream lacking a riparian gallery forest, with low canopy cover, and having low intensity flooding during the growing season of benthic macroinvertebrates. Second, where extensive gallery forest is present, desert streams provide canopy habitat that provides critical daytime refugia for terrestrial insects and longer-lived aquatic insects, thereby enhancing resource availability.

Effects of insect prey on terrestrial consumers

It is well established that aquatic insects can supply terrestrial predators a substantial portion of their diet (Nakano and Murakami 2001, Collier et al. 2002). This contribution can be large along desert streams (Jackson and Fisher 1986, Sanzone et al. 2003). I show that the relationship between bats and aquatic insect prey coincided with asynchrony of aquatic and terrestrial insect prey availability. Correlations between bats and insect prey suggest that bats at Sycamore Creek switch between aquatic and terrestrial insects throughout the year. Asynchronous peaks in aquatic and terrestrial standing stocks corroborate this. Bats likely consume primarily aquatic prey March – June during peak aquatic insect emergence but switch to primarily consuming terrestrial insects July – September (Fig. 13). High aquatic and terrestrial insect availability in June can explain peak bat activity during this month at Sycamore Creek.

At Sycamore Creek, aquatic insect emergence and terrestrial insect biomass were stronger predictors of bat activity than total aerial insect biomass. Further, total standing stocks of aerial insects were not significant predictors of bat capture rate, while aquatic insect emergence and terrestrial insect biomass were. This suggests that aquatic and terrestrial insect prey provide reciprocal food resources to foraging bats throughout the year. Emergent aquatic insects are an important prey resource in the spring while terrestrial insects become more important as aquatic insects availability declines in the summer. Previous studies suggest that bat diet shifts throughout the year in response to aquatic insect availability. For example, in an experimental reduction of aquatic insect emergence along a temperate forest stream in Japan, bats switched from consuming aquatic insects in the spring during peak aquatic insect availability to consuming terrestrial insects in the summer when aquatic insects were less abundant (Fukui et al. 2006).

Diptera composed the majority of aerial aquatic insects during peak aquatic insect availability in April; at both streams dipterans made up 96.6-99.5% of insects on sticky traps (Appendix E: Tables 36 and 37). Similarly, aquatic insect emergence from Sycamore Creek was largely composed of dipterans, primarily Chironomidae and Chaoboridae. A previous study at Sycamore Creek found that Chironomidae made up the majority of aquatic insect emergence (59.7%) followed by Ephermeroptera (19.2%) and Trichoptera (13.7%; Jackson and Fisher 1986). Aquatic insects are an important component of bat diet. For example, aquatic insects, particularly Chironomidae, made up the majority of little brown (*Myotis lucifus)* diet in southern Ontario and Nova Scotia, Canada, and northern New York, USA (Belwood and Fenton 1976). In addition to Chironomidae, lactating females also consumed large quantities of Trichopera and Lepidoptera (Belwood and Fenton 1976). A study in British Columbia found that Trichoptera and Diptera, primarily Chironomidae, composed the majority of the Yuma bat (*Myotis yumanensis*) diet (Brigham et al. 1992). Terrestrial Coleoptera are a common prey item in most insectivorous bat diets in Arizona as well

(Hinman and Snow 2003). Aerial terrestrial insects collected above Sycamore Creek were primarily Coleoptera throughout the year and during peak bat activity in June (75.6%; Appendix E: Table 36).

In contrast to strong asynchrony in aquatic and terrestrial insect prey availability at Sycamore Creek, aquatic and terrestrial insects were generally available in equal proportions at the San Pedro River except in March when aquatic insects made up 96.7% aerial insect biomass. As a result, total aerial insect biomass was the strongest predictor of bat activity, and bat activity was not related to emergent or benthic aquatic insects at the San Pedro River. Further, total aerial insect abundance was the only significant predictor of bat capture rate (Appendix E: Table 35) suggesting that bats track both aquatic and terrestrial insects throughout the year rather than switching between prey resources. Similar to Sycamore Creek, dipterans made up the majority of emergent (23.7 – 92.1%) and aerial (73.7 – 99.1%) aquatic insects at the San Pedro River (Appendix E: Table 37). Aerial terrestrial insects along the San Pedro River were primarily composed of Coleoptera (50-100%; Appendix E: Table 37).

In addition to asynchrony in aquatic and terrestrial insect prey availability influencing bat activity throughout the year, at Sycamore Creek, bats appear to make foraging decisions based on cues related to benthic production and emergence patterns. Both emergence rate and standing stocks of benthic insects were strong predictors of bat activity at Sycamore Creek but not the San Pedro River. This likely resulted from considerably higher aquatic productivity at

Sycamore Creek than the San Pedro River. In a forested stream impacted by wildfire, positive relationships were measured between bats and emergent and benthic insect biomass (Malison and Baxter 2010). Despite high aquatic insect standing stocks at Sycamore Creek, terrestrial aerial insect standing stocks were the strongest predictors of bat activity above the river and in the floodplain. Thus, bats appear to determine if reaches are suitable foraging locations based on latent cues related to aquatic productivity, but more strongly track terrestrial insect standing stocks at Sycamore Creek. My data suggest that bats choose foraging sites using cues related to aquatic productivity and then show remarkable foraging site fidelity based on these cues even as aquatic insect availability declines. On the other hand, at the San Pedro River, bats appear to make foraging decisions based on aerial insect availability. Tracking aerial insect availability appears to benefit bats that forage in extensive grassland habitat as well as directly above the river.

Resource tracking across riparian habitats

At Sycamore Creek, bats tracked aquatic and terrestrial aerial insects similarly above the river and in the floodplain. Here only a narrow band of riparian vegetation separates the stream from the hot desert scrub habitat. Limited foraging habitat therefore concentrated bats to directly above the river and the near floodplain. In contrast to Sycamore Creek, bats tracked aerial insects differently above the river than in the floodplain at the San Pedro River. Bat activity was similar above the San Pedro River and in the floodplain, but lower insect standing stocks in the floodplain resulted in more steeply sloped regressions between bats and aerial insect prey in the floodplain. Correlations between bats and aquatic and terrestrial aerial insect prey above the river had slopes less than one. Further, aerial insects were stronger predictors of bat activity in the floodplain than directly above the river. These findings are likely related to the extensive riparian habitat along the San Pedro River, which is significantly wider than along Sycamore Creek. In addition to the extensive gallery forest, grasslands and abandoned agricultural fields surround the stream. While insect standing stocks were much lower in the floodplain than above the river, there was considerably more riparian habitat along the San Pedro River, potentially providing more bat foraging habitat than Sycamore Creek, where the transition to hot desert scrub habitat is near the stream. Further, the open, uncluttered floodplain in comparison to the cluttered airspace directly above the river may be preferred by some species of bats. Clutter caused by dense riparian vegetation can limit bat foraging success by increasing the time required to capture prey and reduce success rate. A previous study by Rainho et al. (2010) found that ground-gleaning insectivorous bats could not reach sufficient energy requirements in dense ground vegetation. On the other hand, dense riparian vegetation provides habitat for terrestrial and long-lived aquatic insects thereby increasing potential prey availability for foraging bats. Perhaps cooler nighttime temperatures promote the migration of aerial insects from dense riparian vegetation alongside the river to the more open floodplain. In fact, large numbers of bats were often observed foraging above the grassland and abandoned agricultural fields (EMH, personal observation).

A study conducted in the Provo River floodplain, Utah, found that most bat species preferred riparian forest and edge habitat over riparian wetlands, agricultural fields, and restored habitats (Rogers et al. 2006). However, bats from the Molossidae family preferred agricultural fields to other riparian habitats (Rogers et al. 2006). I recorded similar rates of bat activity above the San Pedro River and in the floodplain. Many species, including *Myotis velifer*, *Myotis yumanensis*, *Lasiurus cinereus*, and *Eptesicus fuscus* were exclusively captured above the river, while other species foraged both above river and in the floodplain. For example, *Macrotus californicus* and *Antrozous pallidus* were often captured in the floodplain (Appendix E: Table 34). Thus, high abundance of terrestrial prey as well as extensive and diverse riparian habitat support high bat activity both above the river and in the floodplain of the San Pedro River.

Variability in terrestrial consumer and aquatic prey interactions within and between desert streams

Results of this study show considerable differences in the timing and strength of interactions between terrestrial consumers and insect prey in Sonoran Desert streams characterized by differences in insect prey availability. Specifically, I observed strong contrasts in the timing of peak insect emergence, duration of emergence, and adult body size between the 2 study streams. I observed tight coupling between bats and aquatic insect prey in Sycamore Creek, likely in response to high magnitude and long duration aquatic insect emergence. Further, asynchronous peaks in aquatic and terrestrial prey availability set the stage for reciprocal tracking of aquatic and terrestrial resources by foraging bats.

On the other hand, moderate magnitude and punctuated aquatic insect emergence coupled with high terrestrial-insect availability along the San Pedro River contributed to weak associations between bats and aquatic-insect prey. Rather, extensive riparian habitat results in strong relationships between bats and total aerial insect prey, particularly in the uncluttered floodplain.

These results suggest that timing and magnitude of insect prey can affect bat activity along desert streams. Insect prey availability along desert streams is closely tied to the hydrologic regime (Lytle 2002). While the timing of floods during the study period followed long-term hydrograph trends, interannual variability is high in desert stream ecosystems (Sponseller et al. 2010). Therefore, my results may not reflect annual patterns in either stream. For example, during the study period, Sycamore Creek did not have any large monsoon floods. While historically Sycamore Creek receives the majority of floods during the winter months, the largest recorded flood in Sycamore Creek occurred during the monsoon season (685.3 m^3/s, September 5, 1970; USGS NWISweb gage 09510200, Sycamore Creek near Fort McDowell, AZ). Thus, depending on the year and timing of floods; bat insect interactions along Sycamore Creek may be more similar to patterns observed along the San Pedro River. In addition to variation among different types of Sonoran Desert streams, temporal patterns in bat activity may vary among species, and within species across habitats and regions (Obrist 1995, Barclay et al. 1999). Bat activity can also be highly variable at a nightly temporal scales (Hayes 1997, Milne et al. 2005).

Overall, this study suggests interactions between terrestrial consumers and insect prey are tied to life history characteristics of aquatic insects, including rate of aquatic insect emergence, timing of peak emergence, duration of emergence, and size of emergent insects, as well as extent of riparian habitat. Conditions that promote high rates of emergence, extended duration of emergence, large body size of emergent aquatic insects, and asynchrony between peak aquatic and terrestrial insect availability result in strong interactions between terrestrial consumers and aquatic resources. These include limited riparian vegetation, high stream productivity, and extended periods without floods during the growing season. On the other hand, streams characterized by extensive gallery forests, low productivity, and large monsoon floods tend to be associated with weaker linkages between terrestrial consumers and aquatic resources.

CHAPTER 5

EFFECTS OF AQUATIC INSECT AVAILABILITY AND RIPARIAN VEGETATION STRUCTURE ON BAT ACTIVITY

Abstract. Rivers and riparian areas are critical bat foraging habitat, as emergent aquatic insects provide an important food resource. The structural complexity of riparian vegetation could influence bat foraging activity by affecting navigation through airspace. I conducted a large-scale manipulative experiment to examine the response of bats to changes in aquatic insect availability and riparian vegetation structural complexity. Insect abundance and bat activity were measured along two 50-m exclosures set in areas with contrasting riparian vegetation composed of mixed cottonwood, willow, and tamarisk vegetation (CW-TAM; high structural complexity) versus tamarisk but no cottonwood or willow vegetation (TAM; low structural complexity). Exclosures effectively reduced aquatic insect abundance and bat activity in both the riparian vegetation types. However, aquatic insect abundance and bat activity were higher along the CW-TAM reach than the TAM reach suggesting that aquatic insect availability influences the location of bat activity rather than structural complexity of riparian vegetation. Transition of riparian vegetation from CW-TAM to TAM may reduce aquatic insect availability thereby having negative effects on insectivorous bats.

INTRODUCTION

Bats make up 25% of all mammal species and serve important ecological roles by controlling insect populations, pollinating flowers, and dispersing seeds

(Kunz and Fenton 2003). Habitat loss, exposure to pesticides and pollution, disease, and human disturbance have led to serious declines of more than half of the bat species in the United States (Bat Conservation International 1995, Hutson et al. 2001, Frick et al. 2010). To improve conservation efforts towards these ecologically important species, more information on bat foraging habitat and dietary requirements is needed (Hinman and Snow 2003). Understanding how food resource availability and riparian vegetation structure influence bat foraging activity will have important implications for bat conservation efforts.

Rivers and riparian areas are recognized as important foraging habitat for bats (e.g., Rydell et al. 1994, Walsh and Harris 1996, Seidman and Zabel 2001). This is assumed to result from high aggregations of emergent aquatic insects, which provide an important food resource to foraging bats (Belwood and Fenton 1976, Racey and Swift 1985, Brigham and Fenton 1991, Brigham et al. 1992, Sullivan et al. 1993, Racey 1998). Experimental reduction of aquatic insects resulted in significant declines in bat activity (Fukui et al. 2006). Previous research along the San Pedro River found strong positive relationships between bats and aquatic insects during the summer dry season (Chapter 3) and throughout the year (Chapter 4).

Riparian vegetation structure may also influence bat foraging activity. Dense riparian vegetation can increase structural clutter negatively affecting bat foraging success by hindering maneuverability and successful prey capture. Clutter, defined as background objects that impede flight and echolocation (Law and Chidel 2002), has been shown to have negative effects on bat activity, especially for small, less maneuverable species with long, thin wings, and frequency-modulated calls (Norberg and Rayner 1987, Brigham et al. 1997, Arlettaz et al. 2001). Vertical clutter from tree trucks and branches, as well as ground vegetation clutter, greatly reduces bat capture success and increases time needed to capture prey (Rainho et al. 2010). In addition to direct effects on bat activity, riparian vegetation structure likely influences the lateral dispersal of aquatic insects within the riverine landscape. Specifically, dense riparian vegetation may concentrate aquatic insects directly above the river, while sparse riparian vegetation structure may promote the lateral dispersal of aquatic insects within the terrestrial landscape.

In this study, I ask what factors influence bat activity in river-riparian landscapes. I hypothesize that bat activity is influenced by availability of emergent aquatic insects. Therefore, bat activity will be depressed where aquatic insect emergence is experimentally reduced. Secondly, if riparian vegetation structure influences bat activity by interfering with bat ability to navigate through dense airspace, bat activity will be reduced at sites with greater structural complexity, regardless of aquatic insect prey availability. Of course these hypotheses may not be mutually exclusive. If riparian vegetation structure indirectly affects bats via alterations to aquatic insect availability and limits bat navigation ability, I expect to find lowest bat activity where aquatic insect emergence is experimentally reduced and riparian vegetation has high structural complexity. On the other hand, bat activity will be highest where there is ambient aquatic insect emergence and low riparian vegetation structure.

Here, I present the results of a large-scale, controlled experiment in which I reduced the emergence of aquatic insects from 2 reaches of an intermittent desert river with contrasting vegetation structure to examine the effects on insectivorous bat foraging activity. Controlled experiments of this nature have only been accomplished once before—in a temperate deciduous riparian forest in Japan (Fukui et al. 2006)—and here the authors did not consider variability in the physiognomy of riparian vegetation. Thus, my experiment is the first of its kind in a desert biome, and the first experiment to cross an aquatic insect manipulation with a factor related to the permeability of riparian vegetation structure to the spatial extent of lateral penetration by insects into the terrestrial landscape.

METHODS

Study site

This research was conducted in June – July 2008 along the San Pedro River at The Nature Conservancy-owned San Pedro River Preserve near Dudleyville, Arizona, USA (32° 56’ N, 110° 45’ W). The San Pedro River is characterized by low and intermittent flows during the spring and summer dry season (April – June), high and variable flows during the summer monsoon (July – September), and moderate and consistant flows during the winter wet season (December – March; Hirschboeck 2009). The river continuously flowed during my study period. Riparian vegetation consists of the Fremont cottonwood-Goodding willow (CW; *Populus fremontii* and *Salix gooddingii*) gallery forest. However, a shift from CW gallery forest to riparian vegetation dominated by tamarisk (TAM; *Tamarix ramosissima)* is evident along some sections of the San

Pedro River (Lite and Stromberg 2005) resulting in a substantial change in riparian vegetation structure at these locations. I selected four 50-m reaches along the San Pedro River, the first 2 reaches consisted of a mixed stand cottonwood, willow, and tamarisk vegetation (CW-TAM), and the remaining reaches consisted of tamarisk vegetation but no cottonwood or willow vegetation (TAM). The contrasting riparian-vegetation composition allowed me to examine how structural characteristics of riparian vegetation influence aquatic insect availability and lateral distributions of insectivorous bats within a desert riverine landscape. The CW-TAM reaches had higher structural complexity or clutter, characterized by the broad-leaf cottonwood tree canopy, dense thickets of tamarisk and willow in the understory, and abundant large woody debris on the ground. By contrast, the TAM reaches had lower structural clutter due to no cottonwood canopy, sparser tamarisk vegetation, and less large woody debris on the ground.

Experimental design

I conducted an experimental reduction of aquatic insects along the San Pedro River and measured the response of bat activity along paired exclosure and control treatments located within reaches of contrasting riparian vegetation structure. Two 50-m long exclosures were constructed from nylon screen (1-mm mesh), supported by a PVC frame, approximately 0.3 meter above the river, at the CW-TAM and TAM reaches (Fig. 17). The TAM reaches were located approximately 300 m downstream of the CW-TAM reaches. Average exclosure width was 5.5 m wide and the exclosures were tailored to each river reach so that the screen covered the entire wetted width of each section of river. Exclosures were lined with rocks to prevent aquatic insects from escaping laterally. Exclosures were deployed 3 June – 29 June 2008. A total of 9 sampling stations were established along each exclosure and control treatment; 3 sampling stations were established at 0- (directly above the river), 25-, and 50-m from the river (Fig. 18). At each sampling station, I acoustically measured bat activity in late May (prior to constructing the exclosure; pre experiment), in early June and late June (during experiment), and in early July (after the exclosure was removed; post experiment).

Aquatic and terrestrial aerial insect abundance was measured using sticky traps at each sampling station 2 times while the exclosures were in place (early June and late June) and 1 time after the exclosures were removed (early July). Sticky traps consisted of 603.2-cm^2 transparent plastic sheets coated with Tanglefoot insect trap coating (Tanglefoot, Grand Rapids, MI, USA), rolled into cylinders, and attached ~1.5 m above the ground to bamboo gardening posts to capture flying insects from all directions. Sticky traps were deployed for 4 consecutive days, after which sticky traps were covered with cellophane and frozen until they were processed in the lab. Insects were subsampled using a 2.54 cm X 2.54 cm grid. All insects were identified in 10 randomly selected squares and categorized as aquatic or terrestrial. Aquatic and terrestrial insect abundance was determined for the 10 squares and multiplied by 9.35 to estimate insect abundance for the entire sticky trap.

Concurrent with measuring insect availability, bat activity was assessed sunrise to sunset using Anabat II bat detecting systems (Titley Electronics, Ballina NSW, Australia). Bat activity is reported as minutes of acoustic activity per night and number of "feeding buzzes" per night. Feeding buzzes consist of a rapid series of pulses produced as a bat approaches potential prey. Using 6 Anabat bat detectors, bat activity was measured at 3 distances from the river (0-m, 25-m, 50-m) in paired control and exclosure sampling stations simultaneously. Bat detecting systems were moved between sampling station pairs nightly to achieve spatial replication.

FIG. 17. 50-m long exclosures along cottonwood-willow-tamarisk (CW-TAM) reach (left) and tamarisk (TAM) reach (right).

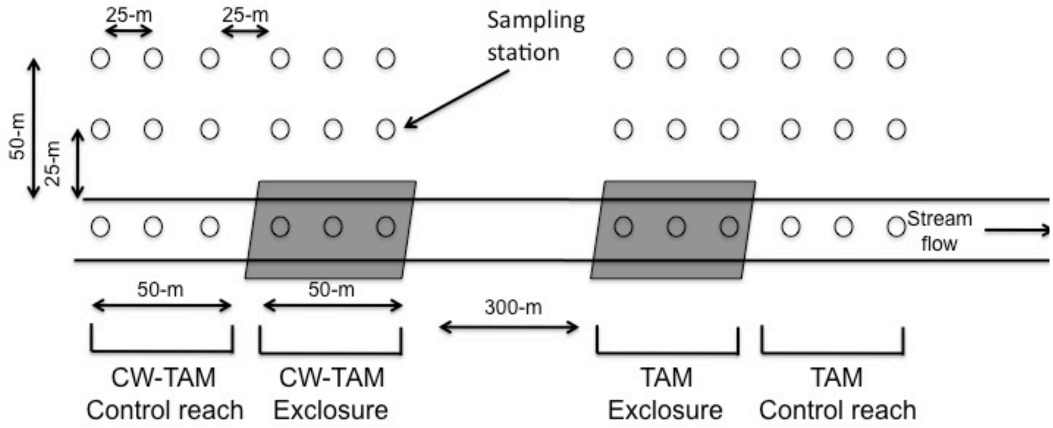

FIG. 18. Schematic diagram showing sampling stations along control and exclosure reaches at cottonwood-willow-tamarisk (CW-TAM) and tamarisk (TAM) reaches.

Pseudoreplication and statistical analysis

By constructing 2 exclosures, 1 in each reach type, I was able to truly replicate treatment (2 exclosures, 2 control treatments), reach type (2 CW-TAM, 2 TAM reaches), and distance from river (4 transects from the river). However, by making 3 measurements of insect availability and bat activity within each reach/treatment location (CW-TAM-exclosure, CW-TAM-control, TAM-exclosure and TAM-control), I am pseudoreplicating sampling stations (Hurlbert 1984). Nevertheless, these pseudoreplicates provide some idea about variability and allow me to test hypotheses about differences observed at but not beyond the four 50-m reach/treatment locations of the San Pedro River included in this study.

The effects of treatment (exclosure vs. control) and reach (CW-TAM vs. TAM) on insect availability and bat activity were examined using 2-way analysis of variance (ANOVA). The response variables for the 4 separate analyses were aquatic insect abundance, terrestrial insect abundance, minutes bat activity, and number of feeding buzzes. For the 2-way ANOVAs, the explanatory variables were treatment and reach. I averaged data collected during the early June and late June sampling periods and excluded data collected during the pre- and post-sampling period thereby sacrificing temporal replication but preserving spatial pseudoreplication within reaches and treatments. The 2-way ANOVAs only included data collected at 0m.

I used 3-way ANOVAs to examine the effects of treatment (exclosure vs. control), reach (CW-TAM vs. TAM), and distance from river (0-, 25-, and 50-m) on insect availability and bat activity. I conducted 4 separate 3-way ANOVAs with the following response variables: aquatic insect abundance, terrestrial insect abundance, bat acoustic activity, and number of feeding buzzes, and explanatory variables: treatment, reach, and distance from river. As with the 2-way ANOVAs, I averaged data collected during the early June and late June sampling periods and excluded data collected during the pre- and post-sampling periods. When necessary, data were transformed to meet assumptions of ANOVA (e.g., normality, equal variance). Pre- and post-sampling data were not included in statistical analysis due to insufficient replication.

In addition to the above analyses that treat pseudoreplicated sampling stations as true replicates, I examined the effects of treatment and reach on insect abundance and bat activity directly above the river using fixed-effects models with 2 main effects (reach and treatment) and no interaction terms, thereby accounting for the pseudoreplicated sampling stations within the replicated main effects. I also used a fixed-effects model with 3 main effects (reach, treatment, and distance from river) but no interaction to account for use of pseudoreplicated sampling stations when examining the effects of treatment, reach, and distance from river on insect abundance and bat activity. Due to low power, these analyses did not show significant effects of treatment or reach. Thus, I report these results only in Appendix F.

RESULTS

Prey abundance

The exclosures effectively reduced aquatic insect abundance directly above the river (at 0-m) at both reaches (2-way ANOVA, treatment effect, F = 11.0, df = 1, P = 0.01; Table 11). Additionally, aquatic insect abundance was significantly higher above the river along the CW-TAM reach than the TAM reach (2-way ANOVA, reach effect, F = 8.1, df = 1, P = 0.02; Table 11). In fact, aquatic insect abundance along the CW-TAM control reach was 2.7 times higher than the TAM control reach during the experiment (Fig. 19). Aquatic insect abundance significantly declined with distance from the river at both reaches (3-way ANOVA, distance effect, F = 53.1, df = 2, $P < 0.001$; Table 12 & Fig. 19). As above, there was also a significant treatment effect (3-way ANOVA, treatment effect, F = 4.3, df = 1, P = 0.049) and a significant reach effect (3-way ANOVA, treatment effect, F = 7.1, df = 1, P = 0.013) with higher aquatic insect abundance at the CW-TAM versus TAM reaches and the control versus exclosure treatments, respectively.

Terrestrial insect abundance did not significantly differ between exclosure and control treatments or between CW-TAM and TAM reaches (Table 11 & 12).

Similar to aquatic insect abundance, terrestrial insect abundance significantly declined with distance from the river (3-way ANOVA, distance effect, $F = 51.3$, $df = 2$, $P = < 0.001$; Fig. 20), but there were significant treatment x distance, reach x distance, and treatment x site x distance interaction terms (Table 12).

TABLE 11. Results from 2-way ANOVAs for aquatic insect abundance, terrestrial insect abundance, bat activity, and feeding buzzes.

Source of Variation	*df*	SS	MS	*F*	*P*
Aquatic insect abundance					
Treatment	1	915531.19	915531.19	10.98	0.011
Reach	1	675483.97	675483.97	8.10	0.022
Treatment x reach	1	357430.44	357430.44	4.29	0.072
Residual	8	667202.77	83400.346		
Total	11	2615648.36	237786.22		
Terrestrial insect abundance					
Treatment	1	4373.52	4373.52	0.57	0.471
Reach	1	2770.35	2770.35	0.36	0.564
Treatment x reach	1	657.56	657.56	0.09	0.777
Residual	8	61149.86	7643.73		
Total	11	68951.29	6268.30		
Bat activity					
Treatment	1	183.07	183.07	0.26	0.625
Reach	1	3757.71	3757.71	5.29	0.05
Treatment x reach	1	3.13	3.13	0.004	0.949
Residual	8	5681.88	710.23		
Total	11	9625.78	875.07		
Feeding buzzes					
Treatment	1	70.08	70.08	2.04	0.191
Reach	1	16.33	16.33	0.48	0.51
Treatment x reach	1	0.75	0.75	0.02	0.886
Residual	8	274.83	34.35		
Total	11	362	32.91		

Notes: Data were ln or ln + 1 transformed.

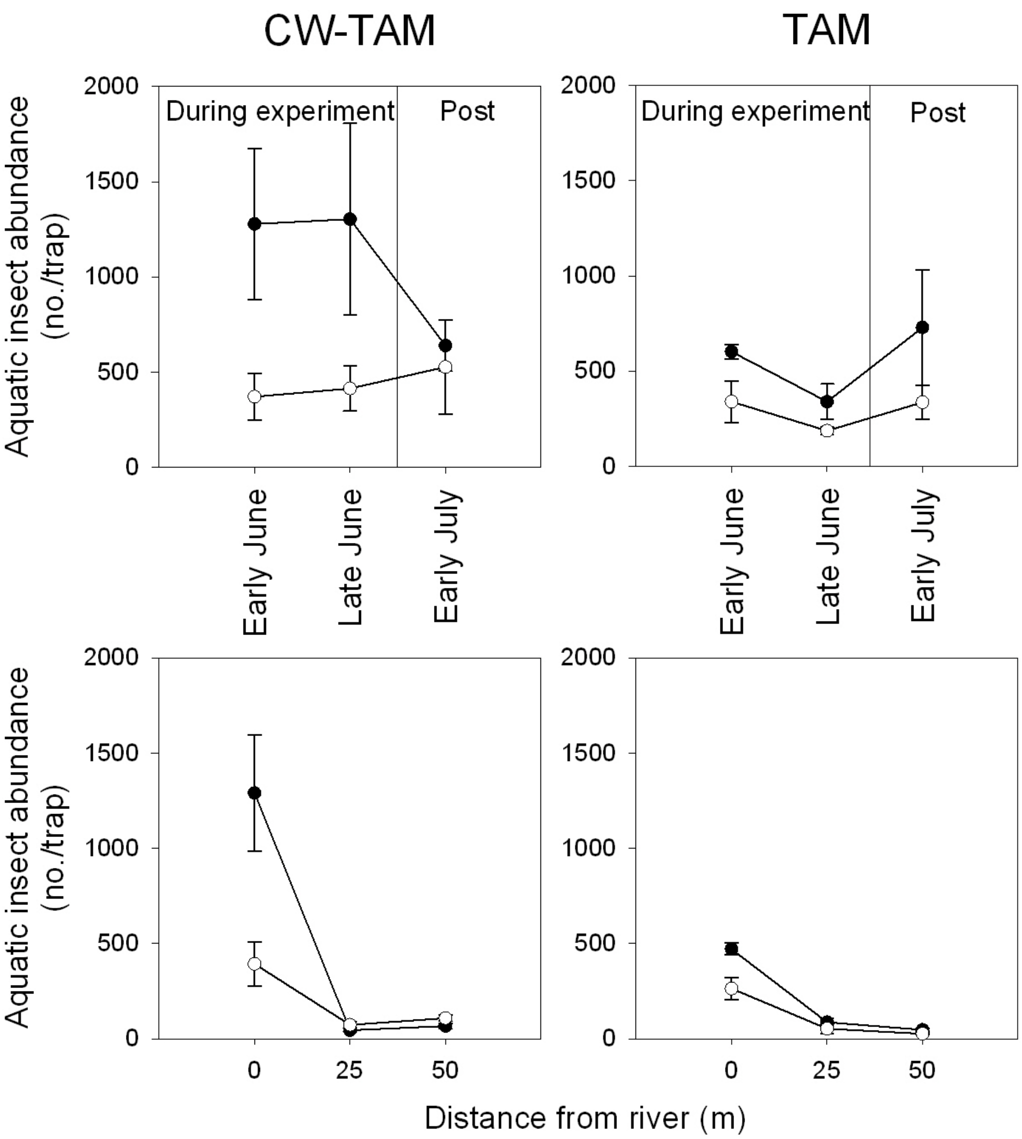

FIG. 19. Mean (± SE) aquatic insect abundance directly above the river (0-m; top panel) while the exclosures were deployed (during experiment) and after they were removed (post) and with distance from the river (bottom panel) along exclosure (open circles) and control (closed circles) reaches at CW-TAM (cottonwood-willow-tamarisk) and TAM (tamarisk) reaches. Data presented in bottom panel were means from the early June and late June sampling periods.

TABLE 12. Results from 3-way ANOVAs for aquatic insect abundance, terrestrial insect abundance, bat acoustic activity, and feeding buzzes.

Source of Variation	*df*	SS	MS	*F*	*P*
Aquatic insect abundance					
Treatment	1	1.56	1.56	4.36	0.049
Reach	1	2.57	2.57	7.14	0.013
Distance	2	38.25	19.13	53.08	< 0.001
Treatment x reach	1	0.93	0.93	2.59	0.12
Treatment x distance	2	1.32	0.66	1.84	0.181
Reach x distance	2	0.95	0.47	1.31	0.288
Treatment x reach x distance	2	1.84	0.92	2.56	0.098
Residual	24	8.65	0.36		
Total	35	56.07	1.60		
Terrestrial insect abundance					
Treatment	1	0.85	0.85	2.91	0.101
Reach	1	0.78	0.78	2.65	0.117
Distance	2	30.14	15.07	51.35	< 0.001
Treatment x reach	1	0.72	0.72	2.44	0.131
Treatment x distance	2	2.11	1.05	3.59	0.043
Reach x distance	2	3.78	1.89	6.43	0.006
Treatment x reach x distance	2	5.97	2.99	10.17	< 0.001
Residual	24	7.04	0.29		
Total	35	51.38	1.47		
Bat activity					
Treatment	1	6.04	6.04	18.05	< 0.001
Reach	1	5.02	5.02	15.02	< 0.001
Distance	2	59.93	29.97	89.62	< 0.001
Treatment x reach	1	1.28	1.28	3.82	0.062
Treatment x distance	2	2.97	1.48	4.44	0.023
Reach x distance	2	5.36	2.68	8.02	0.002
Treatment x reach x distance	2	4.20	2.10	6.27	0.006
Residual	24	8.03	0.33		
Total	35	92.82	2.65		

Feeding buzzes					
Treatment	1	7.05	7.05	14.46	< 0.001
Reach	1	5.14	5.14	10.55	0.003
Distance	2	64.35	32.18	66.00	< 0.001
Treatment x reach	1	7.89	7.89	16.19	< 0.001
Treatment x distance	2	8.65	4.32	8.87	0.001
Reach x distance	2	8.92	4.46	9.15	0.001
Treatment x reach x distance	2	6.01	3.00	6.16	0.007
Residual	24	11.70	0.49		
Total	35	119.71	3.42		

Notes: Data were ln or ln + 1 transformed.

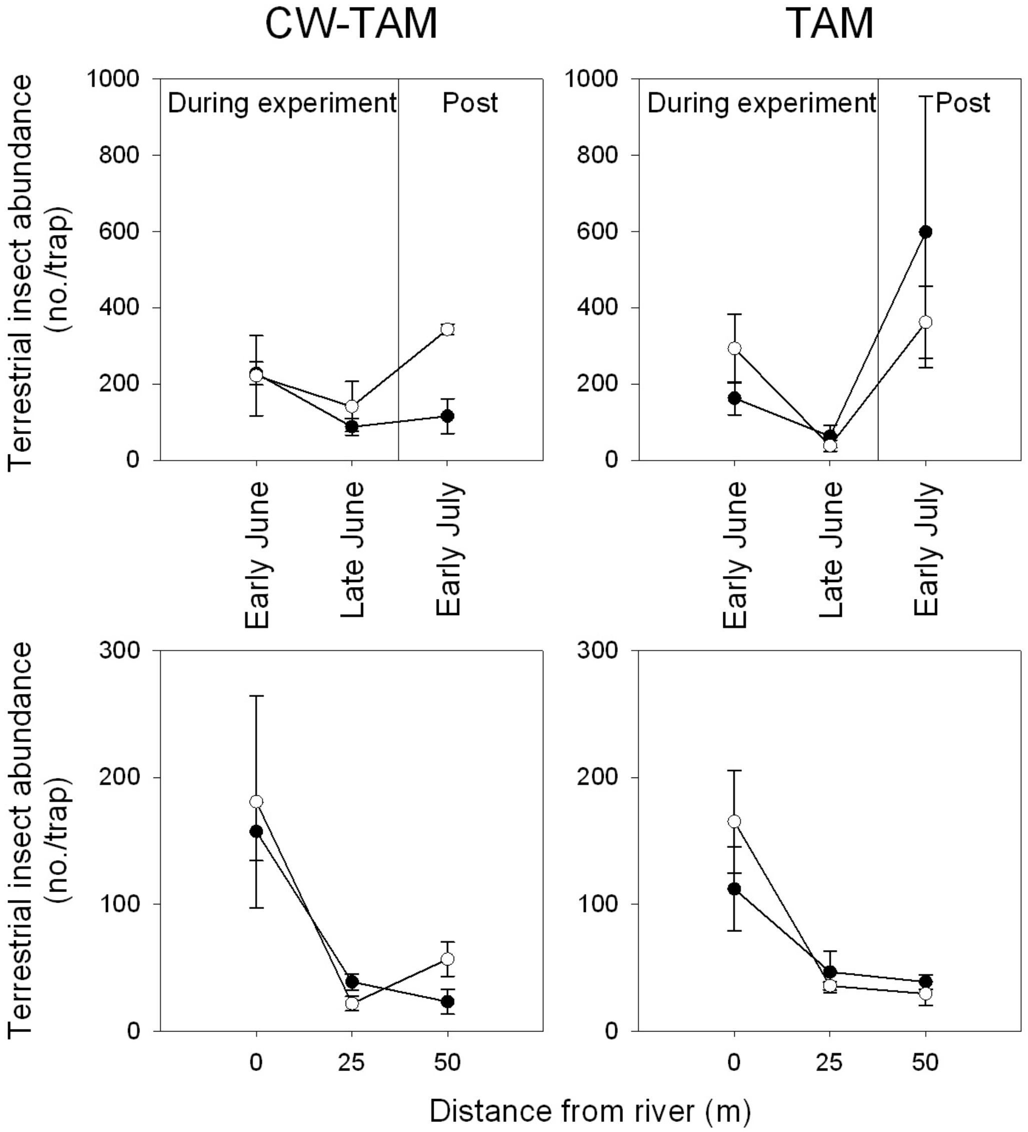

FIG. 20. Mean (± SE) terrestrial insect abundance directly above the river (0-m; top panel) while the exclosures were deployed (during experiment) and after they were removed (post) and with distance from the river (bottom panel) along exclosure (open circles) and control (closed circles) reaches at CW-TAM (cottonwood-willow-tamarisk) and TAM (tamarisk) reaches. Data presented in bottom panel were means from the early June and late June sampling periods.

Bat activity

Minutes of bat activity per night and the number of feeding buzzes recorded directly above the river (0-m) did not vary significantly between the exclosure and control treatments or the CW-TAM or TAM reaches (Table 11). However, bat activity was marginally significantly higher above the river at the CW-TAM reach than the TAM reach (2-way ANOVA, $F = 5.3$, $df = 1$, $P = 0.05$; Table 11). When bat activity measured at 0-, 25-, and 50-m was included in the analysis, there were significant treatment (3-way ANOVA, treatment effect, $F = 18.1$, $df = 1$, $P < 0.001$) and reach (3-way ANOVA, reach effect, $F = 15.0$, $df = 1$, $P < 0.001$) effects (Table 12). Further, bat activity significantly declined, to less than 25 minutes of bat activity per night, by 25-m from the river along both reaches (3-way ANOVA, distance effect, $F = 89.6$, $df = 2$, $P < 0.001$). Number of feeding buzzes was also significantly less along the TAM than CW-TAM reach and along the exclosure versus control treatment, and significantly declined with distance from the river (Table 12). However, there were significant interaction terms for bat activity and number of feeding buzzes (Table 12).

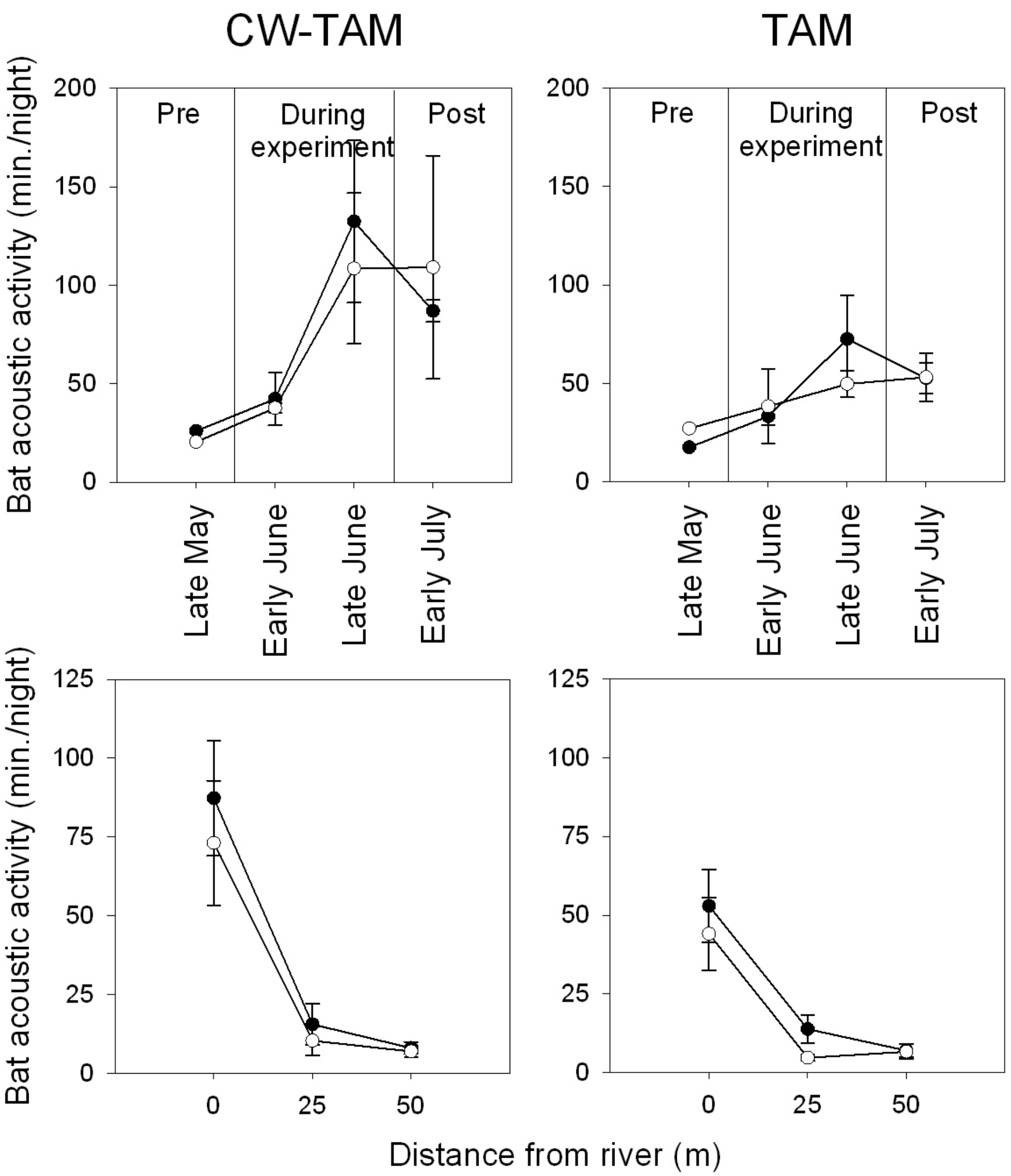

FIG. 21. Mean (± SE) bat acoustic activity directly above the river (0-m; top panel) while the exclosures were deployed (during experiment) and after they were removed (post) and with distance from the river (bottom panel) along exclosure (open circles) and control (closed circles) reaches at CW-TAM (cottonwood-willow-tamarisk) and TAM (tamarisk) reaches. Data presented in bottom panel were means from the early June and late June sampling periods.

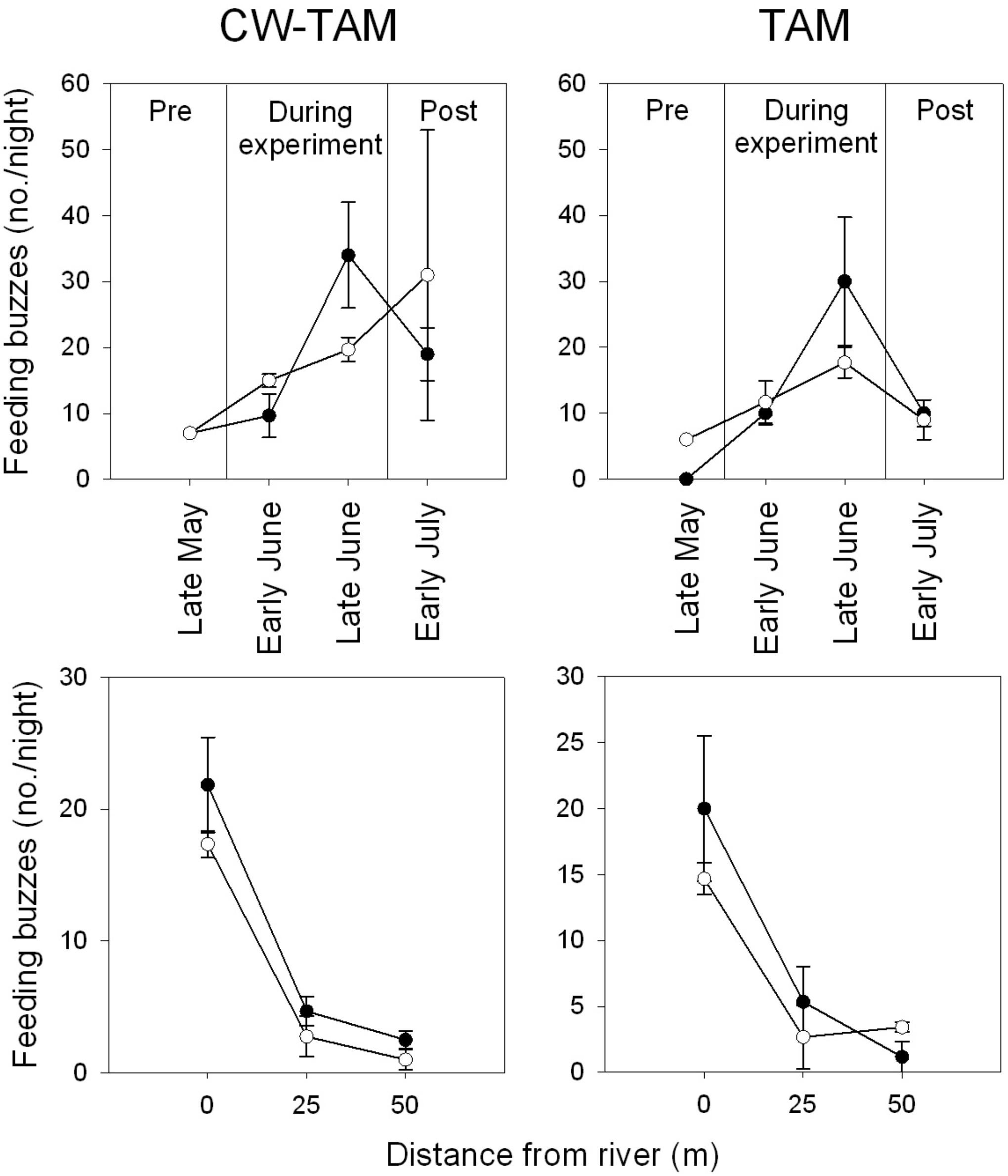

FIG. 22. Mean (± SE) number of feeding buzzes directly above the river (0-m; top panel) while the exclosures were deployed (during experiment) and after they were removed (post) and with distance from the river (bottom panel) along exclosure (open circles) and control (closed circles) reaches at CW-TAM (cottonwood-willow-tamarisk) and TAM (tamarisk) reaches. Data presented in bottom panel were means from the early June and late June sampling periods.

DISCUSSION

Exclosures effectively reduced aquatic insect emergence from the river, significantly depressing bat acoustic activity in both the CW-TAM and TAM riparian habitats. Reach type also significantly affected aquatic insect abundance and bat acoustic activity; however, aquatic insect abundance and bat acoustic activity were higher along the more structurally complex CW-TAM reaches than TAM reaches, supporting the hypothesis that aquatic insect availability and not structural complexity of riparian vegetation affects bat activity. While higher structural complexity associated with CW-TAM riparian vegetation may impede insect capture success (Brigham et al. 1997, Law and Chidel 2002), the significantly higher aquatic-insect availability appears to make foraging in the more cluttered habitat worthwhile. In addition to bats responding to aquatic-insect availability and riparian-vegetation composition, exclosures affected the lateral distribution of bat activity. Exclosures had a larger effect on lateral distributions along the CW-TAM reach, reducing bat activity 10.6 times from 0- to 50-m but only reducing bat activity 6.6 times from 0- to 50-m along the TAM reach. Aquatic insect abundance and bat acoustic activity were higher over the CW-TAM control reach than any other combination, suggesting that mixed CW-TAM stands have higher prey resource availability that bats actively seek out.

Bat activity was 1.6 times higher above the river at the CW-TAM control reach than the TAM control reach despite higher structural complexity along the CW-TAM reaches. While previous studies have shown riparian vegetation to negatively affect bat activity by obstructing flight space and limiting bat navigation ability (Aldridge and Rautenbach 1987, Norberg and Rayner 1987, Grindal and Brigham 1998, Ober and Hayes 2008a), bats appeared to prefer CW-TAM reaches to TAM reaches. Terrestrial insect abundance did not statistically differ between CW-TAM and TAM reaches; however, aquatic insect abundance was 2.7 times higher above the river at the CW-TAM control reach than the TAM control reach, making CW-TAM preferable foraging habitat despite higher structural complexity. Thus, riparian vegetation indirectly affects bats by influencing the availability of aquatic insect prey. Previous studies have shown vegetation to influence the density and distribution of insect prey (e.g., Murdoch et al. 1972). Specifically, cottonwood-willow riparian forests support higher insect abundance than riparian forests composed of tamarisk (Di Tomaso 1998). My results suggest that riparian vegetation structure not only influences aquatic insect abundance but also affects the bats that consume them.

Significantly higher aquatic insect abundance at the CW-TAM reaches than the TAM reaches may be due to several factors. First, the higher quality and quantity of leaf litter produced by cottonwood trees in comparison to tamarisk trees likely provides a more palatable food resource and suitable habitat for larval aquatic insects (Bailey et al. 2001, Kennedy and Hobbie 2004, Whitcraft et al. 2008). Second, cottonwood trees provide more shade than tamarisk contributing to cooler river temperatures with higher oxygen concentrations. Cottonwood trees may also benefit emerged aquatic insects by providing cooler air temperatures, higher quality food resources, and habitat. During the study period, aquatic insect abundance at the CW-TAM control reach was considerably higher than abundance measured ~500-m upstream along a reach with closed CW canopy cover and few TAM trees. Aquatic insect abundance ranged from 1302.8 ± 502.2 to 638.9 ± 134.5 (mean ± SE) along the control CW-TAM reach in late June and July, respectively, while aquatic insect abundance was only 150.6 ± 95.4 and 203.6 ± 192.8 (mean ± SE) in June and July, respectively, at the CW dominated reach upstream (Chapter 4). Perhaps, mixed CW-TAM stands trees facilitate high aquatic insect availability due to warm water temperatures and high aquatic productivity in comparison to CW dominated sites that tend to provide full canopy closure, cooler water temperatures, and lower aquatic productivity. Thus, replacement of CW gallery forest with TAM may have significant consequences to aquatic insect inhabiting desert rivers. Further experimentation with more and perhaps larger replicate exclosures is required to test the generality of how riparian vegetation composition affects aquatic insect availability.

Numerous studies have shown that aquatic insects provide an important food resource to terrestrial consumers, making up 25-100% of the energy supply to these consumers (Nakano and Murakami 2001, Sanzone et al. 2003). Studies have shown that aquatic insects can have strong effects on the abundance, distribution, and behavior of terrestrial consumers (Nakano et al. 1999a, Sabo and Power 2002a, Fukui et al. 2006). Previous research has shown that the presence of emergent aquatic insects has a strong effect on bat foraging activity (Fukui et al. 2006). Specifically, Fukui et al. (2006) measured a significant reduction in bat foraging activity in the spring after experimental reduction of aquatic insect emergence along a temperate deciduous riparian forest stream in Japan. Not only did exclosures reduce bat acoustic activity in the current study, riparian vegetation significantly affected bat activity as well. Thus, transition of mixed CW-TAM gallery forest to TAM dominated riparian vegetation may have negative consequences on organisms that depend on aquatic insects as a food resource.

Caveats

Logistical issues associated with the formidable spatial scale of this experiment only permitted single replicates of each experimental treatment. This is a common occurrence in ecological experiments at large spatial scales (e.g., Schindler 1974, Carpenter 1989). In fact, Fukui et al.'s (2006) experimental reduction of aquatic insects and the response of bats also used a pseudoreplicated experimental design consisting of a single paired exclosure and control reach. Similar to Fukui et al. (2006), I treated sampling stations within units of true replication (i.e., each combination of treatment x reach x distance from river = cells) as replicates. By doing so, I use an inflated number of error degrees of freedom that is inappropriate to determine if the cells significantly differ (*sensu* Hurlbert 1984). Thus, I potentially overestimate the effect sizes (lower error MS), and risk overgeneralizing the strong observed results to the scale of true replication. While the lack of true replicates precludes extrapolation beyond the locations where measurements were taken, the combination of spatial and temporal patterns and the relatively tight error bars affirm that the patterns I observe are not due to chance sampling events in a single cell. This suggests that my conclusions are generalizable to a significant reach of river. Nevertheless, my results must be interpreted cautiously given the misrepresentation of error degrees of freedom in the statistical analysis of the data.

Conclusions

Desert riparian areas provide critical bat foraging habitat (Hinman and Snow 2003). Yet, riparian vegetation is changing along the San Pedro River due to increases in tamarisk dominance along certain reaches (Lite et al. 2005). Increases in tamarisk vegetation along waterways in the southwestern United States has drastically altered riparian vegetation structure (Di Tomaso 1998). Currently, tamarisk is the second most dominant woody species along waterways in the western United States covering over 600,000 ha (Friedman et al. 2005). However, the effects of tamarisk on river-riparian ecosystem structure and function are not well understood. This study suggests that mixed stands of CW-TAM appear to harbor high aquatic insect abundance and these insects appear to be critical prey resources for bats that selectively forage under CW-TAM gallery forest canopies. Reduction of aquatic insect abundance by exclosures in this riparian vegetation type further illustrates the tight coupling between bat and aquatic insects both above the river and up to 50-m into the terrestrial landscape. Thus, transition of mixed stands of CW-TAM to TAM dominated stands may lead to reductions in aquatic insect prey resources thereby having negative consequences on insectivorous bats.

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APPENDIX A

THE FLOW OF DETRITUS ACROSS AQUATIC-TERRESTRIAL BOUNDARIES

This book focuses on the role of detritus on population, community, and ecosystem dynamics. Detritus is an important component of most ecosystems, providing structural (Hansen 2000) and trophic (Minshall 1967) resources to organisms, influencing food web interactions (Wallace et al. 1997), establishing the trophic base of production (Fisher and Likens 1973), and influencing nutrient cycling (Holmer and Olsen 2002). Examining the flow of detritus across ecosystem boundaries can enhance our understanding of the role of detritus on population, community, and ecosystem dynamics (Polis et al. 1997). Here I focus on the flow of detritus across aquatic-terrestrial (AT) ecological boundaries in watershed ecosystems. Stream ecologists have long known that detritus is an important component of stream ecosystem functioning (Odum and de la Cruz 1963, Odum 1969, Fisher and Likens 1973, Hynes 1975) and that streams inherently receive the majority of detritus from adjacent terrestrial ecosystems in the form of autumn shed leaves (Fisher and Likens 1973, Wallace et al. 1997), however, there are few syntheses of detrital flows across AT boundaries in both directions.

In this chapter I characterize the movement of detritus across AT boundaries, emphasizing the origin and directionality, quantity, quality, spatial and temporal variability, and vectors that mediate detrital flows in watersheds. Additionally I discuss the effect of detritus on the structure and function of recipient populations, communities, and ecosystems. I also examine approaches for comparing the relative effect of detrital inputs on recipient ecosystems. These methods include constructing organic matter budgets, large-scale detritus exclusion experiments, and stable isotope techniques. Finally, I identify “holes” in our understanding of the flow of detritus across AT boundaries. To date, the strong seasonal input of leaves to temperate forested streams during autumn leaf fall has been extensively studied in the United States. As a result, most of our knowledge on detritus flows across AT boundaries comes from temperate deciduous forest streams, which are dominated by the unidirectional flow of detritus, primarily leaf litter, from the land to the stream. As a result, many studies have placed little emphasis on the detrital flows from the stream to the land (Table 13). In this chapter I examine how consideration of detritus *quality* and *quantity* influences the relative importance of detritus flow across AT boundaries.

CHARACTERISTICS OF ECOLOGICAL BOUNDARIES

Ecological boundaries consist of physical and biological discontinuities in the landscape. Many terms are synonymous with the term *ecological boundary*, including *edge*, *ecotone*, *interface*, *gradient*, and *transitional zone*. AT boundaries are often described as *riparian zones*. Riparian zones consist of transitional areas between aquatic and terrestrial ecosystems that are characterized by gradients in physical conditions, ecological processes, and biological composition (National Research Council 2002). The structure of these gradients may be abrupt or gradual depending on the location of the riparian zone and the type of flow being measured (Cadenasso et al. 2004). For instance, the boundary between aquatic and terrestrial ecosystems is abrupt when one observes the sharp transition in the presence of surface water; however, the boundary becomes more gradual when subsurface flow is considered. AT boundary structure may also vary depending on the type of detritus flowing across it. For example, AT boundary extent may be ten to hundreds of meters when one considers the width of riparian vegetation separating aquatic and upland habitats, or on the scale of centimeters to meters when one considers the distance a dead terrestrial insect moves when it falls from overhanging vegetation into a stream.

Riparian zones play functional roles by influencing the flow of energy, nutrients, organisms, and detritus between aquatic and terrestrial ecosystems, yet few studies have focused on how ecological boundaries regulate these flows or subsidies (Wiens et al. 1985). Riparian zones can function as *permeable* filters of detrital flows; in other words, only a fraction of detritus passes through the AT boundary (Strayer et al. 2003). For example, not all leaves fall into streams during autumn leaf fall; some are retained and decompose in the terrestrial ecosystem. Alternatively, riparian zones may be *reflective*, in that detritus approaching the AT boundary returns to the patch in which it originates (Strayer et al. 2003). For example, detritus in stream systems lined with bedrock would not be able to enter the hyporheic zone. AT boundaries may also be *neutral*, or have no effect on detritus flow across the AT boundary. AT boundary would have a *neutral* function for a log being transported from the land to the water by a beaver. On rare cases, riparian zones can be *absorptive*, or can *amplify* (transmission > 100%) the flow of detritus (Strayer et al. 2003). Likely the primary function of AT boundaries is to slow and filter the flow of detritus from the land to the stream. For the most part, AT boundaries are *permeable* to the flow of detritus, but depending on the presence of biological or physical vectors, not all detritus will be able to cross the AT boundary. The flow of detritus from the land to the water may be stronger than the flow of detritus in the opposite direction, but this has not been extensively investigated.

Structural and functional components of boundaries are also likely to vary temporally. AT boundary permeability to the flow of detritus can vary over time coinciding with pulses in fish spawning events. Along arid and semiarid streams, the physical location of the AT boundary often varies over time as the stream dries. This will influence when and where algal detritus crosses the AT boundary. Finally, the structure and function of AT boundaries may be specific to the type of detritus flowing across the boundary.

TABLE 13. Flow of detritus across AT boundaries. Detritus flows are mean annual estimates to a variety of biomes. Values represent annual dry mass (g m^{-2} y^{-1}).

Detritus type	Location	Terrestrial biome	Detritus flow	Reference
Detritus originating within a terrestrial ecosystem				
Total litter input	Kuparuk R, Alaska	Tundra	500	Reviewed by Benfield 1997
Total litter input	Canada St, Antarctica	Tundra	0	Reviewed by Benfield 1997
Total litter input	Watershed 10, Oregon, 1974 data	Montane coniferous forest	2789	Reviewed by Benfield 1997
Total litter input	Watershed 10, Oregon, 1973 data	Montane coniferous forest	1204	Reviewed by Benfield 1997
Total litter input	Devil's Club Creek, Oregon	Montane coniferous forest	736	Reviewed by Benfield 1997
Total litter input	Mack Creek, Oregon	Montane coniferous forest	730	Reviewed by Benfield 1997
Total litter input	Lookout Creek, Oregon	Montane coniferous forest	730	Reviewed by Benfield 1997
Total litter input	McKenzie River, Oregon	Montane coniferous forest	218	Reviewed by Benfield 1997
Total litter input	Moisie River, Quebec	Montane coniferous forest	3	Reviewed by Benfield 1997
Total litter input	Sycamore Creek, Arizona	Hot desert	20	Reviewed by Benfield 1997
Total litter input	Kings Creek, Kansas	Grassland	118	Reviewed by Benfield 1997
Total litter input	Ogeechee River, Georgia	Deciduous forest	4363	Reviewed by Benfield 1997
Total litter input	WS 53, North Carolina	Deciduous forest	859	Wallace et al. 1999
Total litter input	First Choice Creek. Quebec	Deciduous forest	761	Reviewed by Benfield 1997
Total litter input	Keppel Creek, Australia	Deciduous forest	745	Reviewed by Benfield 1997
Total litter input	Kings Creek, Kansas	Deciduous forest	726	Reviewed by Benfield 1997
Total litter input	Breitenback, Germany	Deciduous forest	700	Reviewed by Benfield 1997
Total litter input	Creeping Swamp, North Carolina	Deciduous forest	696	Reviewed by Benfield 1997
Total litter input	Satellite Branch, North Carolina	Deciduous forest	629	Reviewed by Benfield 1997

Total litter input	Bear Brook, New Hampshire	Deciduous forest	594	Reviewed by Benfield 1997
Total litter input	Hugh White Creek, North Carolina	Deciduous forest	577	Reviewed by Benfield 1997
Total litter input	Walker Branch, Tennessee	Deciduous forest	565	Reviewed by Benfield 1997
Total litter input	Buzzards Branch, Virginia	Deciduous forest	528	Reviewed by Benfield 1997
Total litter input	August Creek, Michigan	Deciduous forest	448	Reviewed by Benfield 1997
Total litter input	Fort River, Massachusetts	Deciduous forest	384	Reviewed by Benfield 1997
Total litter input	White Clay Creek, Pennsylvania	Deciduous forest	313	Reviewed by Benfield 1997
Total litter input	Beaver Creek, Quebec	Deciduous forest	273	Reviewed by Benfield 1997
Total litter input	Monument Creek, Alaska	Deciduous forest	81	Reviewed by Benfield 1997
Total litter input	Muskrat River, Quebec	Deciduous forest	41	Reviewed by Benfield 1997
Total litter input	Caribous Creek 2, Alaska	Deciduous forest	37	Reviewed by Benfield 1997
Total litter input	Caribous Creek 3, Alaska	Deciduous forest	37	Reviewed by Benfield 1997
Total litter input	Matamek River, Quebec	Deciduous forest	19	Reviewed by Benfield 1997
Total litter input	Rattlesnake Spring, Washington	Cold desert	242	Reviewed by Benfield 1997
Total litter input	Deep Creek, Idaho	Cold desert	3	Reviewed by Benfield 1997
Total litter input	Fuirosos Stream, Spain	Mediterranean	821	Sabater et al. 2001
Wood	Southern Appalachian Streams	Deciduous forest	87	Hagen 2004
DOM	Roaring Brook	Deciduous forest	404	McDowell and Fisher 1976
DOM	Fort River, Massachusetts	Deciduous forest	134	Reviewed by Webster and Meyer 1997
DOM	Satellite Branch, North Carolina	Deciduous forest	49	Reviewed by Webster and Meyer 1997
DOM	Watershed 10, Oregon, 1973 data	Montane coniferous forest	350	Reviewed by Webster and Meyer 1997
DOM	Watershed 10, Oregon, 1974 data	Montane coniferous forest	877	Reviewed by Webster and Meyer 1997
Terrestrial invertebrates	James River drainage, 2nd order streams	Deciduous forest	51	Cloe and Garman 1996, reviewed by Baxter et al. 2005

Terrestrial invertebrates	James River drainage, 2nd order streams	Deciduous forest	23	Cloe and Garman 1996, reviewed by Baxter et al. 2005
Terrestrial invertebrates	James River drainage, 6th order streams	Deciduous forest	7	Cloe and Garman 1996, reviewed by Baxter et al. 2005
Terrestrial invertebrates	Horonai Stream, 2nd order, Japan	Mown grassland	5.1	Kawaguchi and Nakano 2001, reviewed by Baxter et al. 2005
Terrestrial invertebrates	Horonai Stream, 2nd order, Japan	Deciduous forest	14	Nakano and Murakami 2001, reviewed by Baxter et al. 2005
Terrestrial invertebrates	River Nethy drainage, Scotland	Deciduous forest	6.3	Bridcut 2000, reviewed by Baxter et al. 2005
Terrestrial invertebrates	River Nethy drainage, Scotland	Mooreland	4.2	Bridcut 2000, reviewed by Baxter et al. 2005
Hippopotamus feces	Southern Africa	Savanna	100	Naiman and Rogers 1997
Detritus originating within aquatic ecosystems				
Stranded algae	Sycamore Creek, Arizona	Hot desert	102.2	Fisher et al. 1982
Aquatic invertebrates	Sycamore Creek, Arizona	Hot desert	22.4	Jackson and Fisher 1986
Aquatic invertebrates	Horonai Stream, 2nd order, Japan	Deciduous forest		Nakano and Murakami 2001

Notes: The flow of DOM to Roaring Brook includes DOM in groundwater, surface runoff and the leaching of organic matter within the stream. The input of DOM was reported as 343.8 kg over a 77-day period during autumn leaf fall to a 1260 m reach of Roaring Brook. Stream width averaged 3.2 m resulting in a study area of 4032m^2. The input of DOM was scaled up to an annual flow. Webster and Meyer's (1997) measurements for DOM include DOM in groundwater and through fall. The flow of stranded algae was quantified over a 63-day period and scaled up to estimate an annual flow. The measurement of aquatic invertebrates from Sycamore Creek (22.4 g m^{-2} y^{-1}) represents total emergent aquatic insect biomass that enters the terrestrial ecosystems. The proportion directly entering the detrital pathway is unknown.

RESOURCE FLOWS ACROSS ECOLOGICAL BOUNDARIES

Many studies have quantified the magnitude of flows of resources across ecosystem boundaries under the auspices of spatial subsidies. Spatial subsidies are resources (e.g., prey, nutrients, energy, and detritus) that originate in a donor ecosystem and increase the density of plants or consumers in a recipient ecosystem (Polis et al. 1997). Spatial subsidies can affect the recipient ecosystem by increasing the population productivity (increasing survival or fecundity) or by changing the behavior of populations (by promoting aggregation of individuals along the interface between the donor and recipient ecosystems) in the recipient ecosystems (Polis et al. 1997, Sabo and Power 2002a). Detrital subsidies can provide either a trophic resource or a structural resource to recipient ecosystems (Moore et al. 2004). For example, riparian zones provide detritus to stream ecosystems in the form of leaf litter, which is an important food resource for aquatic microbes and macroinvertebrates, and large woody debris, which provides habitat for spawning and rearing fish. In addition to population level effects, detrital subsidies can affect community and ecosystem level processes in recipient ecosystems. Inputs of detritus from terrestrial to aquatic ecosystems can lead to trophic cascades (Nakano et al. 1999b) and can alter rates of whole stream metabolism (Webster and Meyer 1997), and nutrient cycling (Wissmar 1991, Warren et al. 2007). The transport of detritus through space must occur via a vector, either physical or biological. Water and wind are the dominant physical vectors of detritus, while biological vectors include animal movement that transfers detritus across ecosystem boundaries (Cadenasso et al. 2003).

DETRITUS FLOWS ACROSS AQUATIC-TERRESTRIAL BOUNDARIES

There are 5 major developments that led to consideration of detrital fluxes across AT boundaries in whole system organic matter budgets. The first development was by Raymond Lindeman, who recognized the central role detritus (or 'ooze') in his classic study of energy flow and trophic dynamics of Cedar Lake Bog, Minnesota (Lindeman 1942). The second development occurred 15 years later when Howard Odum first considered the flow of terrestrial detritus across AT boundaries. In his energy budget for Silver Springs, Florida, Odum had the forethought to include the input of bread that tourists threw into the water to feed ducks as a detrital input (Odum 1957). The third development occurred when John Teal, who was working on salt marshes along the Georgia coast, quantified the flow of detritus from the water to the land. Teal's (1962) research on Georgia salt marshes revealed how the flow of detritus originating as *Spartina*, the dominate flora in marsh ecosystems, supports a dense terrestrial food web that includes mud crabs, raccoons, and rails.

The final two developments were accomplished by stream ecologists that concentrated on how terrestrial detritus (primarily in the form of leaf litter) affects stream energy flow. In 1967, Wayne Minshall determined that 50-100% of food ingested by primary consumers in Morgan Creek, a small forested stream in Kentucky, was detritus (Minshall 1967). While Minshall did not distinguish between detritus originating within the stream versus detritus originating on land, his work clearly demonstrated the importance of detritus as an energy source. Then in 1973 Stuart Fisher and Gene Likens constructed an organic matter budget for a 1700-m reach of Bear Brook, a small forested stream in New Hampshire. In this study, Fisher and Likens (1973) quantified all inputs of terrestrial detritus to the stream and determined that over 99% of the annual energy budget for this stream came from terrestrial detritus, providing the first quantification of the relative contribution terrestrial derived detritus to stream ecosystem energy budgets.

Oceans

Aquatic and terrestrial ecosystems are closely linked via the flow of detritus across AT boundaries. The boundary between the ocean and land is the earth's largest AT boundary, making up approximately 595,000 km of coastline and 8% of the earth's surface (Polis and Hurd 1996). Detritus originating within the ocean consists primarily of shore drift and carrion, seabird guano, and stranded algae; and primarily moves to the land via hydrologic vectors. Marine detritus can have strong direct and indirect effects on land ecosystems. For example, inputs of seabird guano and carrion can provide an important food resource to a variety of organisms, including flies, beetles, spiders, rodents, and birds. Occasionally, these subsidized consumers contribute to apparent trophic cascades (Polis et al. 2004). For example, flies subsidized by marine detritus are able to increase their abundance, and spiders that prey upon both detritivorous flies and herbivorous insects may shift their predation efforts to the more abundant flies, effectively releasing herbivorous insects from predation pressure. As a result, herbivorous insect abundance increases, leading to increased plant damage when marine detritus is available. On the other hand, detrital inputs of seabird guano and carrion can have a fertilizing effect, contributing to higher rates of plant production along shorelines when these subsidies are available (Anderson and Polis 1999, Sanchez-Pinero and Polis 2000). The reciprocal flow of terrestrial detritus from the land to the ocean can also have strong effects on ocean ecosystem structure and function (Schlesinger and Melack 1981, Hedges et al. 1997). Terrestrial inputs of detritus to the ocean are primarily in the form of dissolved organic matter (DOM) and contribute to the productivity of near coastal ocean habitats (Schlunz and Schneider 2000).

Lakes

Lakes receive large amounts of detritus from the surrounding terrestrial ecosystem (Cole et al. 2007). In fact, inputs of detritus will often equal, if not exceed rates of primary production within the lake itself (Caraco and Cole 2004). Lakes receive inputs of detritus in the form of DOM via hydrologic flow paths, particulate organic matter (POM) such as leaves that blow into the lake and terrestrial prey that fall into the stream. Inputs of DOM primarily contribute to pelagic bacterial respiration, while POM subsidizes zooplankton and benthic macroinvertebrate secondary production (Cole et al. 2006). POM can affect lake food web dynamics by increasing predation on subsidized zooplankton by *Chaoborus* and other planktivorous fishes (Cole et al. 2006). Additionally, detritus, particularly DOM and POM, can supply lake ecosystems with a nutrient source contributing to primary production.

So far I have described detrital subsidies that provide an energetic or food resource to lake ecosystems, but terrestrial detritus can have structural effects on lake ecosystems as well. Suspended POM has been shown to reduce light infiltration in tropical floodplain lakes, thereby affecting predation success in piscivorous fish (Rodriguez and Lewis 1997). Detrital DOM can reduce light attenuation thereby reducing primary production (Williamson et al. 1999). Submerged wood creates structural complexity in lake ecosystems, which provide surface area for periphyton (Lebkuecher et al. 1998), habitat for invertebrates (Smokorowski et al. 2006), and protection from predators (Moring et al. 1989, Everett and Ruiz 1993, MacRae and Jackson 2001).

Cave streams and groundwater

In comparison to lake ecosystems that can receive about half of their energy supply from detrital inputs, cave stream and groundwater ecosystems often receive nearly all of their energy supply from detrital inputs from the terrestrial surface (Jesser 1998, except see Jasinska et al. 1996). Detrital inputs in the form of DOM and POM provide an energy resource for microbes, which in turn support higher trophic levels. For example, microbial biofilms on wood detritus in groundwater ecosystems provide an important food resource to macroinvertebrates, resulting in higher macroinvertebrate densities in groundwater subsidized with woody detritus (Crenshaw et al. 2002).

Streams

While the flow of detritus across most AT boundaries can have strong implications in recipient ecosystems, for the remainder of this chapter I focus specifically on the flow of detritus across stream and land boundaries. Stream ecologists have long recognized that aquatic systems are strongly influenced by the terrestrial environment (Fisher and Likens 1973, Hynes 1975, Wallace et al. 1997, 1999). This is largely attributed to the 1) substantially greater land area of the terrestrial ecosystem in comparison to the aquatic area, 2) greater terrestrial plant biomass in comparison to aquatic algal and plant biomass, and 3) force of gravity pulling detrital material from the watershed down slope towards the aquatic ecosystem. In contrast to the known significance of terrestrial derived detritus in aquatic ecosystems, the importance of aquatically derived detritus in terrestrial ecosystems is still largely undefined. Because stream derived detritus must work against the force of gravity, it is often assumed that this flow is insignificant. Yet, the linkages between aquatic and terrestrial ecosystems are not unidirectional and hydrologic and animal vectors can propagate the movement of detritus to terrestrial ecosystems. While the flow of aquatically derived detritus is often low in comparison to the reciprocal flow, stream derived detritus may provide a critical resource subsidy to terrestrial food webs during times of the year when other sources of energy are in low supply (Sabo and Power 2002b). For example, detrital algae stranded along shorelines is an important energy supply to pigmy grasshoppers during summer drought conditions (Bastow et al.

2002). Before I examine the bi-directional flow of detritus across AT boundaries, it is important to review the role detritus quantity and quality.

DETRITUS QUANTITY AND QUALITY

A central tenet of stream ecology is that the ‘forest feeds the stream’ (Hynes 1970, Cummins 1973, Fisher and Likens 1973, Hynes 1975, Cummins and Klug 1979, Vannote et al. 1980). Thus, most of the detrital inputs to stream ecosystems originate from plant material. Inputs of terrestrially derived leaves and wood can overwhelm local standing stocks of locally derived algae and plants and thus dominate organic matter budgets that support food webs of small streams in forested watersheds. In addition, leaves and LWD provide an important structural component to stream ecosystems. In contrast to the high *quantity* of terrestrial detritus entering streams, this detritus typically has lower *quality* than detritus produced in the stream itself. Detritus quality can be measured as the ratio of carbon to nitrogen (C:N). A high C:N ratio indicates that the detritus provides a low quality food resource, while a low C:N ratio reflects a high quality food resource. For example, algae typically has a lower C:N ratio than terrestrial leaf litter (Table 14). Median periphyton C:N ratio is 12.00 (range 4:1 to 280:1), while median leaf litter C:N ratio is 34.3 (range: 11:1 to 770:1; Cross et al. 2005).

Detritus originating from animal material tends to be of higher quality than plant material (Table 14). On average, the C:N ratio of plants is about 25:1, while the ratio of C:N in herbivorous terrestrial invertebrates is 6.5:1 (Elser et al. 2000). Thus, the flow of terrestrial detritus originating from animals is often very high in quality, making terrestrial invertebrates that fall into the stream an important food resource. While animal derived detritus is a higher quality food resource, it’s important to remember that the magnitude of this flow is often much smaller than detritus originating from plant tissues (Table 13).

FLOW OF TERRESTRIALLY DERIVED DETRITUS TO AQUATIC ECOSYSTEMS

In most small forested stream ecosystems, energy supplied by detritus exceeds in-stream primary production (Hynes 1975, Webster et al. 1995). While some detritus is produced within stream ecosystems (dead macrophytes and algae, animal feces and carcasses, extracellular release of dissolved organic matter), the majority of detritus fueling stream food webs are of terrestrial origin (Fisher and Likens 1973). This includes plant tissues (e.g., leaf litter, dead wood), DOM, and fine particulate organic matter (FPOM) in surface runoff and subsurface flow, and animal feces and carcasses. Organic matter in streams is commonly differentiated based on size. Coarse particulate organic matter (CPOM) is generally greater than 1-mm, FPOM is between 0.5-mm and 1-mm, and DOM is less than 0.5-mm. Once detritus enters a stream, it may be broken down, retained, or transported downstream (Webster et al. 1999). The rates in which these processes occur depend on a number of variables, including detritus type and stream characteristics.

TABLE 14. C:N and C:P ratios of different types of detritus.

Origin	Detritus	Median C:N	Range C:N	*n*	Median C:P	Range C:P	*n*	References
Terrestrial	Leaves	34.30	11-770	13	2720	215-29900	8	Cross et al. 2005
	Leaves	32	7.5-255	406	799	115-5990	413	Elser et al. 2000
	Green leaves	23.90	24-690	4	1100	200-10300	4	Cross et al. 2005
	Wood	113.00	50-1550	7	9850	2280-156000	3	Cross et al. 2005
	FPOM	19.00	11-34	6	365	8-1000	4	Cross et al. 2005
	Herbivores invertebrates	6.4	4.4-21.0	124	73.2	41.9-268.8	27	Elser et al. 2000
	Cicadas		5-6	-	-	-	-	Pray et al. 2009
	DOM	6*	1.5-14.3	-	-	-	-	Brookshire et al. 2005
Aquatic	Periphyton	9.2		267	256		273	Elser et al. 2000
	Periphyton	12.00	4-280	7	379	25-16500	7	Cross et al. 2005
	Invertebrates	6.0		38	114		40	Elser et al. 2000
	Fishes	5.31	4.2-6.5	2	47.60	26-94	2	Cross et al. 2005

*Mean value shown.

Large woody debris

Large woody debris (LWD) is a general term referring to woody material (e.g., logs, branches) that enters stream ecosystems. Inputs of woody detritus can range in size from small twigs to entire trees and often make up a large proportion of detrital inputs to stream ecosystems, particularly in streams draining mature forests (Anderson and Sedell 1979). While inputs of LWD may be a dominant detrital input to forested streams, this detrital flow is insignificant in desert, grassland, and glacial streams (Minshall 1978). LWD enters stream ecosystems via physical vectors (i.e., a tree falling into a stream during a heavy wind storm). However, LWD may also enter stream ecosystems via biological vectors. For example, beaver (*Castor canadensis*) can mediate the movement of significant amounts of wood across land-stream boundaries having large effects on stream hydrology, channel morphology, nutrient cycling, decomposition, and plant and animal interactions (Naiman et al. 1986, Naiman et al. 1988).

Wood has a high lignin and cellulose content; therefore, the breakdown of woody debris is quite slow. As a result, wood does not provide an important food resource to stream food webs. Nevertheless, the consumption of wood has been reported in several aquatic insects including caddisflies, stoneflies, craneflies, midges, and beetles (e.g., Anderson and Sedell 1979, Pereira et al. 1982). While LWD does not provide a substantial food source to stream ecosystems, LWD does stabilize the stream channel, increase the retention of smaller organic matter via debris dams, and provide an important substrate for aquatic macroinvertebrates and biofilm development by microbial organisms. The primary effects of increased hydrologic stability provided by LWD inputs are increased sediment retention and greater pool formation (Keller and Swanson 1979, Bilby 1984). Secondarily, stabilized hydrologic conditions lead to increased bank protection, which is important in riparian forest development (Fetherston et al. 1995, Abbe and Montgomery 1996).

Retention of organic matter, particularly CPOM, by debris dams can affect stream populations and communities. For example, retention of CPOM allows stream detritivores, particularly macroinvertebrate shredders, more time to process CPOM before it is transported downstream (Bilby and Likens 1980). This is especially relevant in temperate, deciduous forested streams that receive a short pulse of litter fall in the autumn. The majority of CPOM processed by shredders becomes FPOM that subsequently becomes available for other functional feeding groups. For example, additions of LWD can contribute to higher densities of collector-gathers and collector-filters that feed on FPOM produced by shredders (Richardson and Neill 1991, Lemly and Hilderbrand 2000).

The input of LWD to stream ecosystems also increases the complexity of the stream channel, providing a variety of habitat patches for aquatic organisms. In particular, LWD directly contributes to the formation of pools, an important habitat for salmon (Fausch and Northcote 1992). Accordingly, salmon, primarily coastal cuttthroat (*Oncorhynchus clarki clarki*) and juvenile coho (*O. kisutch*), biomass and abundance was higher along stream reaches with LWD in comparison to stream reaches where LWD was removed (e.g., Fausch and Northcote 1992, Beechie and Sibley 1997, Wright and Flecker 2004). In addition to population and community level effects, LWD influences ecosystem processes. CPOM, primarily in the form of leaves, provides the energy base to many stream ecosystems. The retention of this material behind debris dams allows streams to retain an important energy supply. Thus metabolic processes by stream organisms would be substantially reduced if this material were quickly transported downstream.

Leaf litter

Leaf litter generally makes up the largest component of detrital inputs to temperate deciduous forested streams (69 to 80%; Wallace et al. 1995), the majority of which occurs during autumn leaf fall (Benfield 1997). Leaf litter inputs tend to be quite variable, ranging from 0 to 4363 g m^{-2} y^{-1} in tundra and deciduous forests streams, respectively (Table 13). The primary vector for leaf litter transport across the AT boundary is physical, resulting from the wind blowing loose leaf litter down-slope into streams ecosystems (Benfield 1997).

Leaf litter provides both an important structural and trophic resource for aquatic organisms (Richardson 1992, Dudgeon and Wu 1999). Leaf litter modifies stream structure by forming leaf packs, accumulations of leaves and other organic matter at the upstream side of obstructions in the stream (e.g., cobbles, boulders, large woody debris), or by depositing on the streambed in areas with slower flows (e.g., pools). Leaf packs can provide an important habitat for a variety of stream organisms, including refuge to macroinvertebrates attempting to avoid fish predation (Holomuzki and Hoyle 1990, Reice 1991). For example, lab experiments have shown that habitat structure provided by leaf packs results reduced fish predation on amphipods in comparison to gravel or sand habitats (Holomuzki and Hoyle 1990).

Leaf litter provides an important food resource for macroinvertebrates in stream food webs. However, leaf litter is only available as a food resource to macroinvertebrates after it has been conditioned (e.g., Cummins 1974, Minshall et al. 1985). Typically occurring within the first 24-hours of a leaf entering a stream, leaf-conditioning is a multi-step process that involves the rapid chemical leaching of soluble organic and inorganic material. Leaching is followed by the colonization of the leaf by microbial organisms, primarily fungi and bacteria. Microbial colonization enhances leaf litter palatability and nutritional value for macroinvertebrate shredders (Cummins 1974, Gessner et al. 1999). Through feeding activities, particularly ingestion of leaf material and production of feces, shredders serve an important function in stream ecosystems by converting larger leaf particles (CPOM) into smaller particles (FPOM; Cummins et al. 1989). FPOM provides an important food source to other types of macroinvertebrates, specifically collector-gatherer functional feeding groups (see Fine Particulate Organic Matter section below).

Fine particulate organic matter

FPOM in streams is composed of leaves, wood, macrophytes, and periphyton; and largely results from the breakdown of leaf litter. Leaf litter breakdown contributes to FPOM production via the physical fractionation of leaf litter and the production of feces from macroinvertebrate shredders that are consuming leaf material. FPOM originating in terrestrial ecosystems (e.g., breakdown of leaf litter on the forest floor) can enter stream ecosystems via surface and subsurface flow paths. Additionally, microbial uptake of DOM eventually becomes FPOM as microbial biofilms form on leaf, wood, and sediment surfaces. Concentrations of FPOM in streams tend to exhibit strong seasonal variability. Newbern et al. (1981) measured low FPOM concentrations in the winter, moderate amounts FPOM in the summer, and sharp peaks in the spring and fall along the New River, Virginia. They also observed a 15-fold increase in FPOM concentrations following a storm event (Newbern et al. 1981). FPOM inputs to glacial streams also vary seasonally, as glacial melt water is the largest source of particulate organic matter to these streams (Tockner et al. 2002). The primary vector for FPOM across the AT boundary is physical, coming in the form of hydrologic flow paths. Yet, the in stream transformation of leaf litter into FPOM is driven by both physical (shear stress of water) and biological (mastication by macroinvertebrate shredders) vectors. Because the flow of FPOM from the terrestrial ecosystem to the stream is dependent on hydrologic flow paths, this flow will be temporally variable depending on storm events.

Most studies on FPOM in streams tend to focus on the downstream transport of FPOM rather than its role as a food or structural resource (e.g., Hope et al. 1994, Newbold et al. 2005). Yet, FPOM has been shown to contribute to microbial enzymatic activity and growth (Sinsabaugh et al. 1992, Sinsabaugh and Findlay 1995); and provide an important food resource to benthic invertebrates, particularly invertebrates in the collector-gatherer functional feeding group (Wallace and Webster 1996). FPOM could alter the structure of stream ecosystems by increasing the turbidity of the water column and reducing the attenuation of light to the streambed. Not only might this reduce rates of algal productivity, but high concentrations of suspended FPOM in the water column could potentially reduce foraging success of visually oriented predators (Moore et al. 2004).

Dissolved organic matter

DOM is usually the largest pool of organic carbon in stream ecosystems (Fisher and Likens 1973, McDowell and Fisher 1976). Like FPOM, DOM originates during the break-down of soil, plant, and animal organic matter and the majority of DOM in stream ecosystems is likely of terrestrial origin. DOM and POM are distinguished from one another based on size, specifically DOM is less than 0.5 mm (Allan 1995). Most DOM enters streams systems via groundwater and soil water flow paths, but can also enter streams as surface runoff and through fall. As a result, the majority of DOM enters streams during rain events. In the southern Appalachian Mountain region, more than 95% of DOM is exported from the forest to the stream as rain moves through the forest canopy, travels over the forest floor, percolates the soil layer, enters groundwater, and eventually enters the stream, the entire time picking up DOM via leaching from organic matter (Qualls and Haines 1992, Hope et al. 1994). In glacial streams, the majority of DOM enters streams as snow melt (Baron et al. 1991). Decomposition of leaf litter already in the stream ecosystem also releases large amounts of DOM via leaching of soluble organic matter and extracellular release via microorganisms. As a result, DOM inputs to forested streams tend to increase during autumn leaf fall. Leaching of litter inputs made up the largest component of DOM inputs (35%) during autumn leaf fall in Roaring Brook, a small forested stream in Hubbard Brook, New Hampshire (McDowell and Fisher 1976). Similarly, Meyer et al. (1998) determined that leaf litter contributed to 30% of DOM in downstream export. While most of the research on DOM flow in stream ecosystems has been focused in temperate deciduous biomes, likely the majority of DOM in stream ecosystems is of terrestrial origin (e.g., terrestrial vegetation and soil organic matter) regardless of the biome.

The large quantity of DOM in stream ecosystems suggests that this flow of detritus provides an important energy source to stream ecosystems, yet DOM quality is highly variable, ranging from simple labile monomers to complex and recalcitrant fulvic and humic acids (Kaplan and Newbold 2001). While the majority of DOM is not readily available to microorganisms, the smaller labile proportion of DOM does provide an important food source to aquatic bacteria and fungi. Thus, DOM forms the trophic base in many heterotrophic stream ecosystems as labile DOM that is taken up by microorganisms becomes incorporated into higher trophic levels as those microorganisms are ingested by other consumers (Münster and Chróst 1990).

Terrestrial invertebrates and frass

Most studies of detrital inputs to stream ecosystems have focused on detritus originating from plant material (leaves, wood); however, inputs of animal material can provide an important detrital resource to stream ecosystems as well. For example, dead or dying terrestrial invertebrates and frass, fecal material produced by insects, provide a detrital resource to stream ecosystems. While living terrestrial invertebrates may not technically constitute detritus as they fall into the stream, they quickly enter the detrital pool if not immediately consumed after crossing the AT boundary. The flow of terrestrial invertebrates to streams is highly variable both temporally and spatially. The magnitude of this detrital flow is greatest in late spring, summer, and early autumn in temperate zones, coinciding with peak terrestrial plant production and biomass (e.g., Nelson 1965, Edwards and Huryn 1996, Kawaguchi and Nakano 2001, Nakano and Murakami 2001). Accordingly the seasonal variability of this detrital flow is less pronounced in tropical streams that exhibit reduced seasonal variability in plant productivity and biomass (Stout 1980, Cuffney 1988). Spatial variation in the flow of terrestrial invertebrates to streams is strongly related to the type of riparian vegetation along the stream, as different types of riparian vegetation support wide ranges in terrestrial invertebrate species richness and abundance (Mason and MacDonald 1982). As expected, forested and natural grassland streams receive larger flows of terrestrial invertebrates than pastoral or mown grassland streams (Edwards and Huryn 1995, 1996). The flow of terrestrial invertebrates is also greater to streams draining deciduous dominated forests than those draining coniferous dominated forests (e.g., Mason and MacDonald 1982, Allan et al. 2003). The flow of frass is generally small to most stream ecosystems; yet large-scale insect defoliation events could produce large amounts of frass (Seastedt and Crossley 1984). While the flow of frass across AT boundaries has not been quantified, this flow of detritus is likely highest from forested terrestrial ecosystems and expected to primarily occur during warm months when insects are most active. The flow of frass into stream ecosystems is largely passive, as terrestrial invertebrates, feeding in vegetation overlying trees, defecate over the stream, and gravity is the primary vector for frass across the AT boundary.

Terrestrial invertebrates that fall into streams provide a high quality food source to many fish consumers, making up to 50% of fish annual diets and energy budgets (Wipfli 1997, Kawaguchi and Nakano 2001, Nakano and Murakami 2001). Several studies suggest that many fish may preferentially consume terrestrial invertebrates over aquatic food sources (Hubert and Rhodes 1989, Young et al. 1997). This has been attributed to the generally larger size of terrestrial invertebrates in comparison aquatic invertebrates (Nakano et al. 1999a) and because terrestrial invertebrates floating on the water surface are more visible to predacious fish than aquatic invertebrates, which are often, camouflaged along the streambed. This is particularly evident on sunny days, when the dark shadow of floating terrestrial invertebrates is highlighted against the bright background of the sky. In addition to having population level effects on fish abundance, biomass, and behavior, detrital inputs of terrestrial invertebrates can affect stream and terrestrial food webs (see Large Scale Detritus Exclusion Experiments section below).

Terrestrial invertebrates also produce frass that enters stream ecosystems, but rather than providing a food resource to fish, frass primarily supplies a nitrogen (N) source to streams, potentially affecting aquatic invertebrate density (Kochi et al. 2004). While the flow of frass is generally small to most stream ecosystems, large-scale insect defoliation events could produce a large pulse of frass and potentially alter N cycling in terrestrial and aquatic ecosystems (Seastedt and Crossley 1984). For example, frass from gypsy moth caterpillars can result in increases in stream N concentrations (Christenson et al. 2002, Townsend et al. 2004).

Animal carcasses and feces

Generally animal carcasses and feces make up a small input of detritus to most stream ecosystems and most of the studies that measure the role of animal fecal and carcass input focus on agricultural streams. Yet, these inputs could be important in streams draining other land use types as well. For example, hippopotamus (*Hippopotamus amphibius*) that forage on terrestrial grasses at night contribute large quantities of feces to the aquatic ecosystems when they return to the aquatic ecosystem during the day. In fact, Naiman and Rogers (1997) estimated that hippopotamuses alone contribute 1 metric ton/ha of detritus to aquatic ecosystems annually. The input of animal carcasses and feces is primarily by biological vectors consisting of movement by the animal producing the detritus.

Studies measuring the role of animal feces and carcasses in relation to stream ecosystems are limited; however, results of these studies do suggest that these inputs can have substantial consequences on stream population, community, and ecosystem level processes. As with detrital inputs of frass, fecal inputs of larger animals can contribute excessive amounts of nutrients, primarily N and phosphorous (P), to stream ecosystems. This is of particular concern in streams adjacent to agricultural lands that support a large number of livestock because increases in N and P input to streams can lead to toxic algal blooms, reductions in dissolved oxygen, fish kills, eutrophication, and an overall reduction in biodiversity (Carpenter et al. 1998). Animal feces may also provide a food resource to stream organisms. For example, del Rosario et al. (2002) measured a 5-fold increase in Chironomidae density in response to cow manure enrichment. Similarly, detrital inputs in the form of animal carcasses will likely release nutrients and provide an energy source as they decompose in the stream ecosystem.

FLOW OF AQUATICALLY DERIVED DETRITUS TO TERRESTRIAL ECOSYSTEMS

The flow of detritus from the stream to the land has not been studied as extensively as the flow of detritus from the land to the stream. Largely this is due to the assumption that the flow of detritus is dominated by gravity which favors the flow of detritus form the land to the stream. Further, the quantity of detritus moving from the stream to the land is generally quite small in comparison to the reciprocal flow (Table 13). However, the quality of stream derived detritus is generally much higher than that of terrestrial detritus entering streams, suggesting a potentially overlooked source of high quality organic matter in recipient terrestrial ecosystems. For this chapter, I describe the five main types of detritus that originate in streams: animal carcasses, emergent aquatic insects, stranded algae, woody debris, and DOM. I focus on salmon carcasses rather than providing a broad overview of all animal carcass movement across AT boundaries (e.g., kingfishers consuming crayfish or frogs originating in stream ecosystems). because, in many ecosystems, these fish make up a major flow of detritus from aquatic to terrestrial ecosystems and because this detritus flow has been extensively reviewed in the literature. In addition to describing the detrital flows from aquatic to terrestrial ecosystems, I describe the magnitude of these detrital flows, when data are available, and discuss the vectors that transport this material from the stream to the land. Additionally I discuss the effects of aquatic derived detritus on terrestrial population, communities, and ecosystems.

Salmon carcasses

Salmon carcasses are a dominant input of marine derived carbon to many terrestrial ecosystems. Annually millions of anadromous salmon return to headwater streams to spawn and die. For example, the Oregon Department of Fish and Wildlife (2008) predicts that 269,300 chinook will return to the Columbia River in 2008. These carcasses then decompose within the stream ecosystem or are transported to the land. While floods can deposit salmon carcasses in riparian zones, the majority of salmon carcasses are transported from the stream to the land by terrestrial scavengers and predators, which include bear, river otter, mink, eagles, and gulls. Most salmon carcasses are deposited within 100 m of the stream, where they are either consumed, cached for later use, or left to decompose. The AT boundary for salmon carcasses is highly permeable to physical and biological vectors that transport this type of detritus. The flow of salmon carcasses from the stream to the land is temporally sporadic, only occurring during summer salmon runs.

In southeast Alaska, over 40 species of mammals and birds feed on Pacific salmon (*Oncorhynchus* spp.), including their carcasses (Willson and Halupka 1995), suggesting that this detrital input can significantly affect the terrestrial populations, food webs, and ecosystem processes. Thus, decomposing salmon carcasses are incorporated into the terrestrial food web at multiple trophic levels.

At the base of the food web, decomposing salmon carcasses release marine derived nutrients (N and P) into the soil, where they become available for uptake by riparian vegetation. Approximately 6.7 kg of P enters the terrestrial nutrient cycle via the decomposition of salmon carcasses transported from the stream to the land by bears alone (Willson et al. 1998). Because most carcasses are deposited within 100 m of the stream, the amount of P entering the terrestrial ecosystem is 6.7 kg/ha, which is equivalent to the standard commercial rate of fertilizer application for evergreens and deciduous trees (Willson et al. 1998). However, this estimate does not include the nutrients that are transported several hundred meters into the terrestrial ecosystem by piscivorous carnivores (Ben-David et al. 1998) or insects that develop in salmon carcasses and migrate further into the watershed (Willson et al. 1998).

Nutrients derived from decomposing salmon carcasses can influence plant production and diversity. For example, Sitka spruce (*Picea sitchensis*) growth rates are three times faster along streams with spawning salmon than streams without salmon (Helfield and Naiman 2001). Overstory riparian vegetation basal area and stem density are greater along salmon spawning reaches than those without salmon (Bartz and Naiman 2005). Decomposing salmon carcasses can also influence the nutrient content of riparian vegetation. For example, the N concentration of devil's club (*Oplopanax horridus*) and ferns (*Dryopteris dilatata and Athyrium felix-femina*) in Alaska is higher along salmon-bearing reaches than reaches without salmon spawning, and some of this difference is attributable to nutrients in salmon carcasses (Ben-David et al. 1998, Helfield and Naiman 2001). While marine derived N content of terrestrial plants is highly variable with distance from the stream and among species, it can make up to 1/3 of total N in plants along salmon spawning streams (Naiman et al. 2002).

Inputs of salmon carcasses to terrestrial ecosystems can affect terrestrial animals by providing an important food resource. Dipterans, primarily calliphoro (blow flies) are a major consumer of decomposing salmon carcasses (Hocking and Reimchen 2006). Moving up a trophic level, detrital salmon carcasses provide an essential food resource to bears and bald eagles during critical stages in their life history (prior to hibernation or long migration events, respectively). Salmon carcasses can make up a significant proportion of the grizzly bear (*Ursus arctos horribilis*) diet. Stable isotope analysis of N in grizzly bear hair and bones revealed that 33% to 90% of N in the diet of bears killed within the Columbia River basin from 1856 to 1931 consisted of marine derived N obtained from the consumption of salmon (Hilderbrand et al. 1996). Further, N in the coastal brown bear (*Ursus arctos*) diet is composed of more than 90% marine derived N acquired either by consuming salmon directly or indirectly via consumption of riparian vegetation (Hilderbrand et al. 1996). Detrital inputs of salmon more than likely have strong effects on several terrestrial populations and communities; however, few studies have explored the effects of this detrital linkage between aquatic and terrestrial ecosystems.

Emergent aquatic insects

Aquatic insects that emerge from streams and disperse laterally into adjacent terrestrial ecosystems are a small, but potentially important flow of material across AT boundaries While the flow of organisms does not constitute detritus per say, the majority of these organisms become part of terrestrial detrital pools shortly after emergence (if not consumed while living). Moreover, many aquatic insects may crawl on shores of rivers to emerge from exuvia, and these exuvia may provide a measurable source of organic matter in terrestrial systems.

Depending on the biome, mean aquatic insect emergence ranges from 10000-20000 individuals m^{-2} y^{-1} (range: 700-156000 individuals m^{-2} y^{-1}; summarized by Jackson and Fisher 1986, Baxter et al. 2005). Jackson and Fisher (1986) measured aquatic insect emergence from Sycamore Creek, an intermittent Sonoran Desert stream, and found that only 3% of the emergent aquatic insect biomass returned to the stream; thus the remainder of aquatic insect biomass crossed the AT boundary to be consumed by terrestrial consumers or enter the detrital pool; however, the fate of these emergent aquatic insects has not been quantified. The emergence of aquatic insects is temporally variable, and is generally highest during summer months in temperate and arid regions, coinciding with peak stream productivity. Numerous studies show that emergent aquatic insects can affect terrestrial consumer abundance (Bastow et al. 2002, Paetzold et al. 2006), behavior (Fisher et al. 1982), and fitness (Bastow et al. 2002), as well as have indirect effects on terrestrial food webs (Henschel et al. 2001, Henschel 2004).

Stranded algae

Algae left stranded on the banks of drying streams are a little studied but potentially important detrital input to terrestrial ecosystems. For example, Fisher et al. (Fisher et al. 1982) measured a 102.2 g m^2 y^{-1} flux of algal export from Sycamore Creek, Arizona. While the input of stranded algae is likely most relevant in arid and semiarid regions, this flow could occur along intermittent or ephemeral streams in a variety of biomes (Bastow et al. 2002, Stanley et al. 2004). The primary vector for stranded algae is physical resulting from drying of the wetted stream channel. This commonly occurs along arid and semiarid streams as the wetted channel retreats during the dry season or during floods when algae is transported onto the floodplain during the flood pulse and subsequently dries as the flows recede.

While the magnitude of this detrital flow is insignificant in comparison to the reciprocal flow of terrestrial detritus along most streams, especially forested streams, the overall energetic and nutritional quality of stranded algae is substantially higher than that of leaf litter (Elser et al. 2000). Thus, algal detritus may provide an important food source for terrestrial organisms. For example, Bastow et al. (2002) found algal detritus to provide a seasonally important food resource to pygmy grasshoppers along a seasonally arid river.

Woody debris

The dominant direction of woody debris is from the land to the stream, yet, woody debris can be transported back across the AT boundary during floods. The primary vector for this detrital flow is hydrologic, as this detrital flow is dependent on the flood magnitude. Few studies have quantified the magnitude of this flow, but it is expected to be highest along larger forested streams. Woody detritus that is deposited along stream banks following floods likely does not provide an important food resource, but could provide habitat for terrestrial organisms. For example, in the Pacific Northwest, woody debris piles along stream banks provide important habitat for birds and small mammals (Steel et al. 1999).

Dissolved organic matter

The flow of DOM is primarily from terrestrial to stream ecosystems via groundwater and soil water flow paths; however, the reciprocal flow also occurs. Depending on the volume and direction of stream flow, DOM can also flow from the stream to terrestrial ecosystem via the same flow paths (Brunke and Gonser 1997). While the ultimate origin of DOM is largely terrestrial (e.g., leaching of leaf litter), some DOM originates within the stream ecosystem. This includes leaching and extracellular release of algae and macrophytes. The vector for DOM is physical, as its transport is dependent on the direction and magnitude of surface and subsurface flowpaths.

QUANTIFYING THE EFFECT OF DETRITUS ON RECIPIENT ECOSYSTEMS

Detritus is highly variable in its composition and availability, which is apt to lead to variable ecological consequences on recipient ecosystems (Moore et al. 2004). Ecologists have used different methods to measure the effect of detritus on population, community, and ecosystem structure and function. Here I discuss three of these methods, which include creating organic matter budgets, detritus exclusion experiments, and stable isotope techniques.

Organic matter budgets

Organic matter budgets are constructed by adding up all of the inputs and outputs of organic matter from a designated area. This area could be a 1-hectare forest plot, a 500-m reach of stream, or the entire catchment of a headwater stream. Organic matter exists in two forms: as living organic matter that is tied up in plants, animals, and microbes, and as non-living organic matter in the form of detritus. Both forms of organic matter can be stored in pools (boxes) and move between these pools as fluxes (arrows) via various vectors (Fig. 23). Organic matter compartment diagrams can be quite complex, but are often simplified for the purpose of understanding the organic matter dynamics in the ecosystem as a whole. When constructing an organic matter budget it is necessary to designate a specific area. Then all inputs and outputs of organic matter into and out of that specified area from various sources are quantified. Once organic matter is within an ecosystem it can be transformed among different pools, respired, or exported out of the ecosystem. Stream ecologists have long considered the lateral input of detritus into the stream ecosystem and include this flow when constructing organic matter budgets (e.g., Fisher and Likens 1973, Webster and Meyer 1997). However, due to the lotic nature of stream ecosystems, the downstream export of organic matter often dominates stream organic matter budgets, while the lateral export of organic matter is often ignored. Terrestrial ecologists often ignore the lateral flow of detritus across AT boundaries as well.

Stream ecologists have used the organic matter budget approach to determine the role of detrital inputs in stream ecosystems by measuring the percentage of the annual energy supply originating from detrital sources. Organic matter budgets have been calculated for a number of stream ecosystems in a variety of biomes and land uses allowing for the comparison of the role of detritus among these different ecosystems. In fact, an entire issue of the *Journal of the North American Benthological Society* was devoted to stream organic matter budgets (Webster and Meyer 1997). In this issue, Webster and Meyer (1997) emphasized the inputs of detritus from the land (i.e., leaves, wood, DOM in groundwater) in their organic matter budget (Fig. 23). This conceptual model is a good starting point that accounts for the dominant flow of detritus into stream ecosystems. To account for the bi-directional flow of detritus across AT boundaries, I propose a modified organic matter budget (Fig. 24). Not only does this model account for the lateral flow of detritus across AT boundaries, but it differentiates among the fluxes and pools of detritus and GPP in aquatic and terrestrial ecosystems.

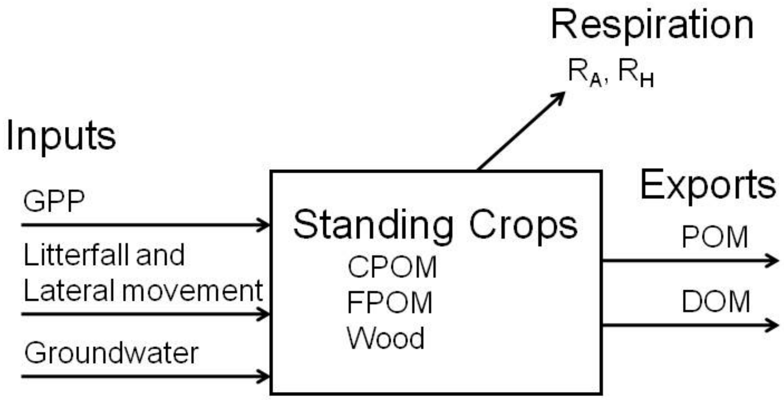

FIG. 23. Organic matter budget for streams proposed by Webster and Meyer (1997). Aside from gross primary production (GPP) and respiration, detritus accounts for the majority of organic matter pools and fluxes in stream ecosystems. R_A and R_H are autotrophic respiration and heterotrophic respiration, respectively. POM is particulate organic matter and DOM is dissolved organic matter.

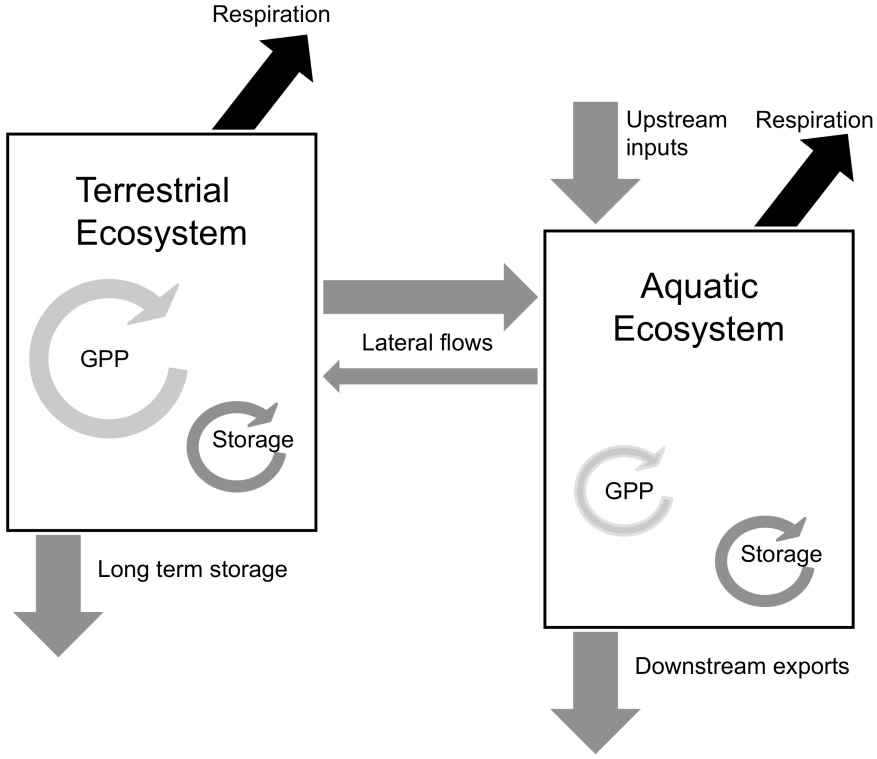

FIG. 24. Organic matter budget emphasizing detrital flows between terrestrial and aquatic ecosystems. Dark gray arrows represent detrital fluxes, light gray arrows represent gross primary production (GPP), and black arrows show respiration.

Shortcomings of Organic Matter Budgets—Despite the importance of organic matter budgets in highlighting the flow of detritus across AT boundaries, the organic matter budget approach has its limitations. First of all, measuring all detrital inputs, exports, and standing stocks is a huge undertaking. Not only is it labor intensive to quantify all of the forms of organic matter, but often times methodologies are not available to accurately quantify certain detrital flows. As a result, organic matter budgets are often simplified by assuming a zero value for certain components of the budget or by determining values indirectly, which could affect the accuracy of calculations. Second, most mass balances assume that the system is in steady state, which may or may not be appropriate. The input of terrestrial detritus is often pulsed throughout the year (e.g., the majority of leaf input to deciduous forest streams occurs during September through November), but an annual organic matter budget would not reveal this temporal variation. Therefore, an annual rate may not reflect a realistic flow rate or pool size in a particular day or season. Third, it is often difficult to delineate an AT boundary when one considers groundwater flow paths, backwater pools, and side channels. This becomes even more difficult in arid and semi arid regions where the AT boundary moves with changes in channel flow (Stanley et al. 1997). Perhaps the strongest limitation of the organic matter budget approach is the failure to account for variations in organic matter quality. Historically, organic matter budgets quantify flows and pools in terms of grams of carbon or calories. The failure to include a measure of quality does not allow for an accurate comparison among ecosystems. For example, the quantity of wood and hippopotamus feces entering streams can be quite similar (Table 13), yet there is a clear distinction in the quality of these two types of detritus, which will affect their contribution to stream ecosystem structure and function. Wood has a very slow breakdown rate and therefore supplies important habitat for stream organisms, while feces are very labile and provide transient habitat at best.

Quantifying Detritus Quality—In an attempt to address the role of detritus quality on recipient ecosystems I compared organic matter budgets for 2 streams: Bear Brook, a temperate deciduous forest stream in New Hampshire, and Sycamore Creek, a desert stream in Arizona (Table 15). These budgets were created by measuring major fluxes and pools of organic matter entering and exiting these stream reaches. I took these organic matter budgets a step further and calculated a C budget for each stream reach using the conversion 1 g dry mass = 0.5 g C (Meyer and Edwards 1990, McTammany et al. 2003). I then calculated a N budget for each stream using C:N ratios gleaned from the literature (Table 14). By doing so I found that 6-times more C originates in Sycamore Creek and moves to the land than in the reciprocal direction (Table 15). On the other hand, the net direction of detritus flow in Bear Brook is from the surrounding forest to the stream (Table 15). In fact, the amount of C entering Bear Brook from the watershed is 203-times greater than the amount of C that leaves the stream. Because stream derived detritus generally has higher quality than detritus originating on land (Table 14) I predicted that the amount of N crossing the AT boundary should become more equivalent in each direction. However, when I examine N flow across Sycamore Creek's AT boundary I find 19-times more N moves from the stream to the land than in the opposite direction. This is largely due to high quality of emergent aquatic insects and stranded algae that originates in Sycamore Creek and moves laterally to the land. At Bear Brook, only 57-times more N enters from the land than leaves the stream in comparison to 203-times more C. So while the difference in N flowing in each direction across Bear Brook's AT boundary is dampened in comparison to the flow of C, I still conclude that in forested systems the flow of detritus from land to streams dominates in terms of quantity and quality. Terrestrial detrital inputs are huge (594 g m^{-2} y^{-1} to Bear Brook) to forested streams and overwhelm the higher quality of detritus originating in the stream (Table 15). By contrast, in desert systems the flow of detritus from land to stream pales in comparison to the reciprocal flow, both in terms of quantity and quality. This is likely an artifact of extremely large differences in primary productivity between forested and desert stream ecosystems (Webster and Meyer 1997).

TABLE 15. Carbon and nitrogen budgets for Sycamore Creek and Bear Brook.

	Sycamore Creek				Bear Brook				
	DM	C	N	Reference and notes	DM	C	N	Reference and notes	C:N ratio
Physical characteristics									
Stream order	5			Jones et al. 1997	2			Fisher and Likens 1973	
Watershed area (ha)	505			Jones et al. 1997	130			Fisher and Likens 1973	
Strembed area (m^2)	33.1			Stanley 1993, Jones et al. 1997	5877			Fisher and Likens 1973	
Inputs ($g\ m^{-2}\ y^{-1}$)									
GPP	1888	944	103	Grimm 1987	3.5	1.8	0.2	Findlay et al. 1993	9.2
Groundwater DOM	-	-	-		95	48	8	McDowell and Likens 1988	6
Lateral inputs									
Litterfall and lateral movement	19.6	9.8	0.3	Schade 1995	594	297	9	Fisher and Likens 1973	32
Emergent aquatic insect return	0.7	0.4	0.1		-	-	-		6
Standing crops (g/m^2)									
Wood > 1 mm	-	-	-		530	265	2	Fisher and Likens 1973	113
CBOM > 1 mm (not including wood)	5.2	2.6	0.1	Schade 1995	610	305	10	Fisher and Likens 1973	32
FBOM < 1 mm	104	52	3	Grimm 1987	53	27	1	Fisher and Likens 1973	19
Hyporheic FPOM	39	20	1	Jones et al. 1995	-	-	-		19
Exports									
Autotrophic respiration ($g\ m^{-2}\ y^{-1}$)	944	472	0	50% of GPP	1.75	0.88	0	50% of GPP	

Benthic heterotrophic respiration (g m^{-2} y^{-1})	372	186	0	Grimm 1987, RE - 50% GPP	101	51	0	Hedin 1990	
Hyporheic respiration (g m^{-2} y^{-1})	3259	1630	0	Jones et al. 1995	-	-	0		
Downstream exports									
Particulate transport (kg/y)	11900	5950	313	Grimm 1987	1700	850	45	Fisher and Likens 1973	19
Dissolved transport (kg/y)	506000	253000	42167	Jones et al. 1996	514	257	43	Fisher and Likens 1973	6
Lateral exports									
Algae drying on stream bank (g m^{-2} y^{-1})	102.2	51.1	5.6	Fisher et al. 1982	-	-	-		9.2
Aquatic insect emergence (g m^{-2} y^{-1})	23.1	11.6	1.9	Jackson and Fisher 1986	3.4	1.7	0.3	Iwata et al. 2003	6
Total inputs to stream (g m^{-2} y^{-1})	1908	954	103		693	347	17		
Total exports from stream (g m^{-2} y^{-1})	522600	261301	42488		2317	1161	88		
Total T to A flow (g m^{-2} y^{-1})	20	10.2	0.4		689	345	17		
Total A to T flow (g m^{-2} y^{-1})	125	62.7	7.5		0	1.7	0.3		

Notes: Dry mass values for Sycamore Creek are in ash free dry mass and dry mass values for Bear Brook are reported as dry mass. Dry mass values were converted to g carbon using g C = 0.5 g dry mass (Meyer and Edwards 1990, McTammany et al. 2003). Nitrogen content was determined using C:N values obtained from Table 14. Aquatic insect emergence for Bear Brook estimated as 3.4 g m^{-2} y^{-1} using an average emergence rate of 9.43 mg m^{-2} y^{-1} calculated by Iwata et al. (2003). Average aquatic insect emergence rate was measured in 2 streams draining riparian deciduous forests in southwestern Hokkaido Japan. Aquatic insect emergence rate was measured in May. DM = dry mass; C = carbon; N = nitrogen.

Large scale detritus exclusion experiments

Detritus plays an important role on population, food web, and ecosystem level structure and function. Thus a strategy to quantify the effect of detritus on recipient ecosystem function and structure is to exclude the flow of detritus from the land to the stream or vice versa. I discuss two such experiments that exclude the flow of detritus from the land to the stream. The first experiment took place at Coweeta Hydrological Laboratory in the southern Appalachian Mountains, North Carolina. Here leaf litter inputs were excluded from a forested, headwater stream by placing a 1.2-cm mesh net over the first 180 m of this stream (Wallace et al. 1997). Additionally, a 1-cm mesh fence lined both banks, preventing lateral inputs of detritus into the stream. The canopy was installed in 1993, effectively reducing leaf litter inputs by more than 95% (Wallace et al. 1997). Additionally, all sticks and logs were removed from the stream in 1996, and 1998, respectively. This multi-year litter exclusion study resulted in significant changes in benthic macroinvertebrate community, especially macroinvertebrates dependent on leaf litter as their primary food source (i.e., shredders and collectors-gatherers); (Wallace et al. 1997, 1999). In mixed substrate habitats, habitats where the streambed is composed of sand, gravel, pebble, and cobble substrates, shredder, collector-gatherer, predator, and total benthic macroinvertebrate abundance and biomass were significantly reduced in response to litter exclusion. Only scrapers and filterer functional feeding groups, which are less dependent on detrital food resources, showed no response to litter exclusion. Exclusion of litter effectively reduced predator abundance and biomass by indirectly reducing their food supply, which includes shredding macroinvertebrates. Further, Wallace et al. (1997, 1999) showed that leaf litter exclusion reduced secondary production of benthic macroinvertebrates in mixed substrates and showed strong bottom-up effects through multiple trophic levels, including primary consumers through predators.

Leaf litter does not only affect stream populations and food webs, but can affect energy flow and nutrient cycling in stream ecosystems as well. For example, higher rates of microbial respiration (Tank and Webster 1998) and nutrient retention (N and P) (Webster et al. 2000) have been measured in the litter exclusion stream in comparison to a reference stream. Leaf litter affects stream ecosystem level processes primarily by supplying a nutrient source and slowing the flow of water, thereby allowing more time for nutrient transformation (i.e., microbial uptake), and by providing habitat for colonization by microbes (Webster et al. 2000). By excluding leaves from streams, nutrients would otherwise be quickly taken up by microbes colonizing leaf litter, are available for other heterotrophic processes, such as microbial respiration (Tank and Webster 1998).

The second large-scale exclusion experiment involved the installation of a 50-m plastic greenhouse over Horonai Stream, a forested, headwater stream in the Tomakoma Experimental Forest located in Hokkaido, Japan, which effectively reduced inputs of terrestrial invertebrates to the stream (Nakano et al. 1999b). This caused a dramatic shift in fish (Dolly Varden, *Salvelinus malma*) predation from terrestrial invertebrates to benthic aquatic invertebrates. By significantly reducing aquatic invertebrate biomass, particularly scraper and collector-gather functional feeding groups that feed on algae, algae biomass significantly increased (Nakano et al. 1999b). The resulting trophic cascade provides evidence for the strong role detrital resource subsidies can play in influencing stream ecosystem processes. Further, reduction of aquatic invertebrates reduces aquatic insect emergence thereby limiting a food source to terrestrial consumers (e.g., birds, bats, lizards, and spiders), having both direct and indirect effects on terrestrial food webs (reviewed by Baxter et al. 2005).

Stable isotopes to source carbon in stream ecosystems

Organic matter budgets and detrital exclusion experiments have been very effective for comparing the relative contribution of detritus among different ecosystems and showing the effects of detritus on population, community, and ecosystem structure and function, respectively. However, these methods are not effective at differentiating among the different forms of detritus (e.g., leaves vs. algae) that are assimilated by different consumers. Large disparities exist between the quantity and quality of terrestrial and aquatic derived detritus, thus there are potentially differences in the quantity of detritus eaten by primary consumers (Mayer and Likens 1987, Hall et al. 2001); however, little is known about how much detritus is actually assimilated from each source by aquatic consumers (but see McCutchan and Lewis 2002). Stable isotopes can in some cases provide robust estimates of assimilation from different energy flow pathways. Carbon stable isotopes (^{13}C) have been widely used in many stream ecosystems to determine the origin of C in top consumers (Junger and Planas 1994, Doucett et al. 1996, Grey et al. 2001, Thorp and Delong 2002). A consistent finding in many of these studies is that, despite dominance of organic matter pools by detrital inputs from terrestrial systems (McCutchan and Lewis 2002) or macrophytes (Hamilton et al. 1992), top predators assimilate a disproportionate amount of C derived from algae. Unfortunately, in some systems, carbon stable isotopes are limited in their ability to separate aquatic and terrestrial derived C, due to high seasonal and spatial variation in algal $\delta^{13}C$ signatures and variation in the $\delta^{13}C$ signature of dissolved inorganic carbon (e.g., Finlay 2001). Work by Doucett et al. (2007) suggests that stable isotopes of hydrogen (^{2}H) may provide wider separation between aquatic and terrestrial sources of organic matter and thus, a more robust tool for reconstructing energy flow pathways between terrestrial and aquatic food webs, but these methods need additional testing before being generally applicable.

EFFECTS OF STREAM SIZE, BIOME, AND LANDUSE

The magnitude of terrestrial detritus flow varies spatially, both longitudinally as one moves from headwater streams to large rivers (Vannote et al. 1980) and with different biomes or landuse types (Table 13). Detrital inputs are expected to be most important to streams that have forested riparian vegetation and low rates of primary production (Vannote et al. 1980). These include forested headwater streams that receive large annual inputs of detritus in the form of leaves and wood from the surrounding forest, but have low rates of primary production due to heavy shading by riparian vegetation. Terrestrially derived detritus also likely fuels the trophic base of large rivers because DOM contributes to high turbidity in the stream column and reduced light attenuation, thereby limiting in stream primary production. In comparison to small headwater streams that receive the majority of their detritus as lateral transfer from the riparian zone during autumn leaf fall, large rivers receive the majority of their detritus via downstream transport or lateral inputs from the floodplain during floods. Even wide, shallow rivers that should be less dependent on detrital inputs to form their energy base, such as the New River, a sixth order stream in Virginia, receive 60% of their energy supply from detrital inputs (Hill and Webster 1982). In general, forested streams are significantly more dependent on the flow of detritus from terrestrial ecosystems than streams draining areas with less vegetation, such as desert (Schade and Fisher 1997), glacial (Naiman and Link 1997), and pastoral streams (Hagen 2004). On the other hand, the flow of stream derived detritus, primarily in the form of stranded algae and emergent insects, likely has strong effects on terrestrial populations and communities along desert streams. Regardless of stream size, biome, or landuse, the flow of detritus across AT boundaries clearly has strong implications on recipient ecosystem populations, food webs, and ecosystems.

SUMMARY, CONCLUSIONS AND FUTURE DIRECTIONS/SPECULATIONS

Stream ecologists have long considered the importance of terrestrial detritus to stream ecosystems, but the quantity and quality of detritus originating in aquatic ecosystems has received little attention. Out of 51 studies that quantified the flow of detritus across stream-land boundaries, 49 measured the flow of detritus from the land to the stream (Table 13). Largely this was in the form of leaf litter to deciduous forest streams. In these systems, the large quantity of detritus that moves from terrestrial to stream ecosystems drowns out the effects of detrital flows from stream to terrestrial ecosystems. Even though recent studies have shown that detritus originating within the stream, primarily in the form of fish carcasses and emergent aquatic insects, can have strong effects on terrestrial consumers by providing a high quality trophic resource during critical periods of the year (Nakano and Murakami 2001, Naiman et al. 2002). The few studies that have quantified the flow of detritus from the stream to the land occurred along a single desert stream; these studies suggest that the flow of stream derived detritus may have larger effects in desert biomes than temperate biomes due to higher in-stream productivity relative to terrestrial productivity (but see Marczak et al. 2007) and the higher quality of stream derived detritus in comparison to terrestrial derived detritus (Table 14). Clearly this deserves further investigation due to the limited number of studies that have examined the detrital flow from the stream to the land.

In addition to the relatively minimal work on the flow of detritus across desert stream AT boundaries, the role of detritus in other biomes has received even less attention. In some biomes the flow of detritus across AT boundaries may be insignificant. For example, tundra and boreal streams are characterized by low annual rates of gross primary production and leaf litter inputs (Webster and Meyer 1997) suggesting that detrital flows across AT boundaries do not have large effects in these biomes. The flow of detritus across tropical stream AT boundaries is among the least studied, despite detritus potentially having large consequences due to the high productivity of tropical terrestrial and aquatic ecosystems. Not only might the direction, quantity, and quality of detritus flow vary in comparison to temperate deciduous forest and desert streams, but the largest contrast will probably be in the temporal variability of detrital resources. The flow of detritus is a temporally pulsed resource to deciduous forest streams and desert riparian areas in the form of autumn leaf fall and stranded algae, respectively. Tropical streams, on the other hand, are characterized by continuous detrital flows; these include leaf litter input (reviewed by Benfield 1997) and aquatic insects (Corbet 1964). The lower diversity of invertebrate shredders in tropical streams (Dudgeon 1989, Pringle and Ramirez 1998, Rosemond et al. 1998, Dudgeon and Wu 1999, Dobson et al. 2002) may also have consequences on the effects of terrestrially derived detritus on tropical stream ecosystems. Conducting research on the role of detritus on terrestrial and aquatic ecosystems in multiple biomes is necessary to develop a general framework for understanding detrital flow across AT boundaries. Further research is also necessary to determine how quantity of detritus influences recipient populations, communities, and ecosystems.

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APPENDIX B

EFFECTS OF DETRITUS ON FOOD WEB STRUCTURE IN MARINE, FRESHWATER, AND TERRESTRIAL ECOSYSTEMS

ABSTRACT

Detritus is a central feature in marine, freshwater, and terrestrial ecosystems. Despite the ubiquity of detritus, ecologists have largely ignored its role in influencing food web structure. We used a meta-analysis approach to ask four questions about how detritus affects food web structure in a wide variety of ecosystems. First, what is the effect strength of detritus on primary producers, detritivores, herbivores, and predators? Second, what functional role does detritus serve for consumers (energetic, habitat, or both)? Third, how does the effect of detritus on consumers vary between aquatic and terrestrial ecosystems? Fourth, does detritus catalyzes top down control of predators on living plant tissue? We found that detritus has strong positive effects on primary producers and consumers in a wide range of ecosystems types. Detritus has a positive direct effect on detritivores by providing an energetic resource and both an energetic resource and habitat (refuge from predators). Detritus has equally strong positive effects on herbivores and predators, driven by a positive direct effect of habitat. Detritus has positive effects on consumers in both aquatic and terrestrial ecosystems with stronger effects in terrestrial ecosystems. Finally, we find more support for the notion that detritus determines trophic structure from the bottom up via fertilization of primary producers rather than by top down indirect effects on predators. These results suggest that detritus determines trophic structure and may set the stage for trophic dynamics in a variety of ecosystem types—even in the portion of the food web linked most strongly to living plant tissue as its primary energy source.

INTRODUCTION

Detritus is at the center of classic descriptions of energy flow like Lindeman's classic 'food cycle' (1942) and is considered to be a key determinant of rates of primary production and species richness (Yee *et al.* 2007), the biomass of consumers dependent on detritus as an energy source (Dilling et al. 1998, Findlay et al. 1998, Halaj and Wise 2002), and trophic dynamics (Polis and Strong 1996, Cebrian 2002, Moore et al. 2004). Further, detritus can have "fertilization effects" on primary producers by providing nutrients, increasing growth rates of plants, and stimulating secondary productivity from the bottom up (Spiller et al. 2010). By contrast, other theories of trophic structure hold that detrital pathways actually provide the energy necessary for consumers to depress the abundance, biomass, or density of herbivores, thereby releasing primary producers to prosper (Polis and Strong 1996, Spiller et al. 2010). In this view, detritus actually catalyzes trophic cascades and facilitates a green world.

Detritus can play multiple roles in determining the structure of food webs. Detritus exerts direct effects on consumers by providing the sole energetic resource for these animals. For example, dissolved organic carbon (DOC) provides an energetic resource for microbes (Jonasson et al. 1996, Teira et al. 2009) and seston is an energetic resource for some aquatic insects (Perry and Sheldon 1986). Detritus provides habitat and increases the energetic resources (detritivore biomass) for predators of these consumers, thereby having direct and indirect effects on higher trophic levels, respectively. In particular, large, recalcitrant forms of detritus like woody material from trees and kelp or sea grass may not only provide habitat but modify existing habitat for top predators (Bilby and Bisson 1992). Detritus also provides substrates and refugia for herbivores that consume “epi-detrital” plant material (Mulholland et al. 2000) and nutrients for primary producers (Spiller et al. 2010). Many of the aforementioned roles of detritus on trophic structure are well understood in isolation, yet there has been little synthesis of their effects in a broader community context.

Detritus may have different effects on trophic structure and dynamics in different types of ecosystems as a result of variation in detrital production, decomposition, and turnover rates. For example, aquatic and terrestrial ecosystems vary in several fundamental ways, including food web structure and function (Cyr and Pace 1993, Chase 2000, Shurin et al. 2006), population density and structure (Cyr et al. 1997), and energy flow (Hairston and Hairston 1993). Numerous studies have similarly shown clear differences in the source, quantity, quality, timing, and decomposition of detrital resources in aquatic and terrestrial ecosystems (Enriquez et al. 1993, Cebrian 1999, Cebrian and Lartigue 2004, Nowlin et al. 2008). For example, detrital resources tend to decompose and turnover quickly in aquatic ecosystems but tend to persist longer in terrestrial ecosystems (Chase 2000, Shurin et al. 2002, Shurin et al. 2006, Nowlin et al. 2008). The effect of these differences in the way detritus is processed on the relative trophic structure of aquatic and terrestrial food webs is unresolved.

Finally, detritus may determine the strength of top-down control of plant biomass by enhancing the production and abundance of predators (Polis and Strong 1996, Halaj and Wise 2002, Spiller et al. 2010). Detritus is often absent from many textbook theories of trophic structure, including green world (HSS: Hairston et al. 1960) or exploitation ecosystem hypotheses (EEH: Oksanen et al. 1981). HSS and EEH advocate strong roles for predators in maintaining trophic structure and living (green) plant biomass. The omission of detritus from HSS and EEH is curious given that detritus can support greater predator biomass and longer food chains than would be supported by primary productivity alone (Hairston and Hairston 1993). Green world theory suggests that biomass should increase only at alternating trophic levels with increases in the supply of basal resources (living plant productivity). Little effort has been made to quantify the effects of detritus on primary producers and consumers (detritivores, herbivores, and their predators) in a similar framework.

In order to understand the multiple functional roles and the diverse impacts of detritus at different trophic levels throughout the food webs of different types of ecosystems, we performed a meta-analysis that examined how primary producers and consumers responded to detritus manipulation (manipulative studies) or to gradients in the quantity of detritus (mensurative studies). Specifically, we synthesize data on the effects of detritus on a diverse set of marine, freshwater, and terrestrial ecosystems ranging from open ocean (e.g., marine snow) to agricultural systems (e.g., mulch) and rivers (e.g., large woody debris). We ask four questions about the functional roles of detritus in food webs: 1) How strong are the effects of detritus on primary producers and consumers that use this resource?, 2) Does detritus serve primarily as an energetic resource or habitat for consumers occupying higher trophic levels, and 3) How does the effect of detritus vary between aquatic and terrestrial ecosystems?

Finally, we ask whether detritus catalyzes top down control of predators on living plant tissue. We accomplish this task by analyzing studies in our database that measured the effect size of detritus on primary producers, herbivores, and detritivores coupled by a common predator to test a pair of competing hypotheses. First, if detritus fuels trophic cascades via apparent competition and predators have strong effects on herbivores and plants mediated by detritivores (Polis and Strong 1996), then effect sizes of detritivores would be positively correlated with predators. Moreover, effect sizes of detritivores and predators would be negatively correlated with herbivores and positively correlated with primary producers. In other words we expect strong top-down control of herbivores by predators fueled by detrital energy, thereby releasing primary producers from herbivory leading to a green world. Alternatively, detritus may simply have strong universal "bottom-up" effects on all upper trophic levels in the detrital or green channel. Here we would predict strong positive effects on primary producers and all upper trophic levels. Further, we would expect the effect size of detritivores to be positively correlated with effect sizes of plants, herbivores, and predators. Thus, the key evidence differentiating these hypotheses is the correlation between detritivores and herbivores. A positive correlation indicates strong bottom up control, whereas a negative correlation provides support for detrital-fueled trophic cascades in the green channel.

METHODS

Study system—Definition of detritus

Detritus is the non-living organic matter in an ecosystem generated by the growth and production of living organisms (*sensu* Moore et al. 2004). We considered detritus to include various types of plant tissue (e.g., leaf litter, dead wood, decomposing macrophytes, algae), animal tissue (e.g., carrion), dead microbes, feces (e.g., manure, dung, fecal pellets, guano, frass), as well as organic products secreted, excreted, or exuded from organisms (e.g., extra-cellular polymers, dissolved organic matter, extra-cellular matrix, mucilage).

A meta-analysis of the effects of detritus on primary producers and consumers

<u>Literature search criteria</u>—Our literature search was conducted using the *Web of Science* database (1955 – 2010) and the following search terms: [TYPE OF DETRITUS] AND (Produc* OR biomass OR abundance OR richness OR diversity). We repeated the above search with each of 27 types of detritus (Table 16). This search produced over 100,000 papers. To reduce the number of papers, we repeated the above search, and sorted the results 2 ways: by order of descending number of citations and by publication date. We then selected the top

5 most cited papers in each detritus category and the 5 most recently published papers that had appropriate data for each type of detritus, thus allowing us to sub-sample the available literature in a consistent way. Some types of detritus did not have 5 papers with appropriate data; for these categories we used all available publications in that category with the appropriate data.

To further increase the number of papers that examine the effects of detritus on multiple trophic levels, we conducted a second *Web of Science* search with the following search terms: [TYPE OF DETRITUS] AND (Herbivore AND Predator) AND (Produc* OR biomass OR abundance OR richness OR diversity). As above, we sorted the results by order of descending number of citations and by publication date. We then selected the top 5 most cited papers and 5 most recently published papers that had appropriate data for each type of detritus. The two searches resulted in 84 papers.

Our sub-sampling methods could potentially exacerbate the "file-drawer" problem inherent in meta-analysis—where studies with insignificant results go unpublished and are thus not included in a meta-analysis. To diagnose the potential for this bias we estimate fail-safe numbers for each of our effect sizes to quantify the number of unreported (non-significant) results that would be needed to alter any conclusions reached from records sub-sampled following our citation-based methods (Rosenberg et al. 2000). Fail-safe numbers were calculated as:

$$N = \frac{\left(\sum w_i Z_i\right)^2}{t^2_{\alpha[v]}} - \sum w_i \qquad (1)$$

where N is the fail-safe number, w_i is the weight of the i^{th} record, Z_i is the effect size of the i^{th} study, t is the value of the Student's t-distribution with v degrees of freedom (Rosenberg et al. 2000).

Meta-analysis design and data structure—For each paper included in our analysis ($N = 84$), we identified the *type of user* as primary producer, detritivore, herbivore, predator, and 'mixed' (i.e., all three consumers combined), and recorded the response to detritus. Primary producer responses to detritus included chlorophyll *a* concentration, plant biomass, plant height, plant density and number of leaves. Consumer responses to detritus were abundance, biomass, density, or richness. Papers examining the effects of detritus on primary producers and consumer abundance, biomass, and density were combined prior to calculating effect size; papers examining the effects of detritus on consumer richness were combined in a separate analysis.

We classified the *functional role* of detritus on consumers *a priori* as food (hereafter, 'energetic'), habitat, or both. This classification was done based on details reported in each paper (e.g., where the authors discussed consumption of the resource, or use of the resource as habitat). Where the authors did not report such details, we made *ad hoc* classifications based on our interpretations of the relationships between consumers and resources in the system. In most cases, classifications were simple. For example, large woody debris in streams provides habitat for fish (e.g., Fausch and Northcote 1992) and most invertebrates (Lemly and Hilderbrand 2000, Johnson et al. 2003, Hrodey et al. 2008). Similarly, organic soil is an energetic resource and habitat for soil detritivores and only habitat for predators (Ponsard and Arditi 2000). Nevertheless, some classifications were more difficult, and here we used two qualitative guides for classification purposes: 1) relative size of consumer and resource particles, and 2) edibility of resource. Large size of detritus relative to consumer coupled with relative high edibility of the resource (or a fraction of the resource) led us to classify the functional role of detritus as "both" (energetic and habitat). Examples of such classifications include drift kelp (in marine and beach ecosystems), leaf litter for small invertebrates, soil, marine snow, and carrion. Where the size of detritus was large relative to consumer of interest and the resource edibility was low, we classified the role of detritus as 'habitat'. Examples of such classifications include: predators or herbivores using detritus for cover or nesting, and detritivores using wood as structural habitat. Detritus with small relative size to consumer and high edibility was classified as "energetic." Examples include DOC in freshwater ecosystems and soluble organic carbon (SOC) in soil ecosystems.

To examine if the effects of detritus on consumers vary between aquatic and terrestrial ecosystem types, we classified each paper as aquatic, terrestrial, or transitional. Aquatic ecosystems consisted of fully submerged habitats. For example, streams, lakes, and the deep sea. Terrestrial ecosystems included agroecosystems, grasslands, and forests. Transitional ecosystems (e.g., salt marshes, intertidal mangrove forests, beaches) were not included in the comparative analysis due to low sample size relative to those in the aquatic and terrestrial categories.

Some papers in our meta-analytic database included several types of usable data (e.g., abundance and density, response data for multiple taxa) so we created an individual record for each "new" piece of data (Wolf 1986, Gurevitch et al. 1992). This resulted in 490 records from 84 papers. We then averaged effect sizes within each *type of user* or *functional role* classification for multiple records from identical experiments in the same paper to reduce the possibility of pseudoreplication.

Effect size estimation—For each record, we extracted data necessary to calculate an effect size. Generally, data were reported as standardized mean difference (means and standard deviations) and correlation coefficients (F-test, R^2, Spearman R). Unfortunately many papers were rejected because they omitted necessary data (e.g., several papers published F-values without reporting *df* or *MS*). When means and standard deviations were presented as graphs rather than tables, we digitized the graph using DataThief II (www.datathief.org) or GetData (www.getdata.com) to obtain the necessary data. When results were reported as a time series, we only included data from the last time step in our analysis (Gurevitch et al. 1992). For each record with appropriate data, we converted the various effect size measures into a common one, R, which we then converted to Z (Rosenberg et al. 2000). This allowed us to use a multitude of different types of studies that presented different metrics of effect size (standardized mean differences, F ratios, T-tests, and correlation coefficients). In papers reporting means and standard deviations for simple manipulative experimental designs, we calculated the standardized mean difference, d_{ij}, for each record as:

$$d_{ij} = \frac{\overline{X}_{ij}^{-D} - \overline{X}_{ij}^{+D}}{s_{ij}} \tag{2}$$

where $\overline{X}_{ij}^{+D}$ was the mean for the control group (with detritus), $\overline{X}_{ij}^{-D}$ was the mean for the experiment group (detritus removed), and s_{ij} was the pooled standard deviation of the control and experimental group, which was calculated as:

$$s_{ij} = \sqrt{\frac{\left(N_{ij}^{-D} - 1\right)\left(s_{ij}^{-D}\right)^2 + \left(N_{ij}^{+D} - 1\right)\left(s_{ij}^{+D}\right)^2}{N_{ij}^{-D} + N_{ij}^{+D} - 2}} \tag{3}$$

Here, N_{ij}^{+D} was the number of individuals in the control group, N_{ij}^{-D} was the number of individuals in the experiment group, s_{ij}^{+D} was the standard deviation for the control group, and s_{ij}^{-D} was the standard deviation for the experiment group. Standardized mean difference was then converted to R as:

$$R = \sqrt{\frac{d_{ij}^2 N_{ij}^{-D} N_{ij}^{+D}}{d_{ij}^2 N_{ij}^{-D} N_{ij}^{+D} + \left(N_{ij}^{-D} + N_{ij}^{+D}\right) + \left(N_{ij}^{-D} + N_{ij}^{+D} - 2\right)}} \tag{4}$$

Formulas used to convert other test statistics to R, where standardized mean differences were not available (i.e., F, t, etc.), are outlined in Table 17. We then converted R to the standard effect size measure, Z_i viz:

$$Z_i = \tfrac{1}{2} \ln\left(\frac{1+R}{1-R}\right) \tag{5}$$

where the variance and weights of the effect size for each study are $v_i = \frac{1}{n-3}$ and $w_i = \frac{1}{v_i}$, respectively, and n was the sample size of each individual record. Records were weighted because meta-analysis combines studies with different sample sizes and variances.

Quantifying structure and estimating cumulative effect size and total heterogeneity—We introduced structure in our meta-analytic dataset using three separate analyses on different subsets of our data: 1) A single factor analysis quantifying the effects of detritus on primary producers and standing stocks of different types of consumers (detritivores, herbivores, predators, and "mixed" consumers), 2) A similar single-factor analysis but using species richness of different types of consumers as the response variable, 3) A single factor analysis that examined the impacts of detritus on standing stocks of higher-level consumers (i.e., detrititvores, herbivores and predators) while accounting for the functional role of detritus in each case, and 4) A single factor analysis quantifying differences in the effects detritus on the standing stock of consumers (plants and higher level consumers including our "mixed" category, combined) between aquatic and terrestrial ecosystem types (transitional ecosystems excluded). Thus, we divided our data into two response variables (standing stocks and richness). Using the remaining standing stock records we then examine the impact of functional role on the entire subset of standing stock records (univariate analysis). Finally we examine the effects of Functional Role within Type of User classification, and the effects of Ecosystem Type on further reduced (but still large) subsets of the standing stock records.

In each of these analyses we carried out four meta-analytic procedures: 1) estimation of a mean and 95% confidence interval of effect sizes, 2) test for significant total variation in effect size magnitude, 3) estimation of the statistical significance of categorical structure (e.g., Type of User) in the dataset, and 4) estimation of the mean and 95% confidence intervals of the effect sizes within each level of the categorical structure of the data. In all cases, effect sizes (Z_i) and weights (w_i) for individual records from identical experiments in the same paper were averaged within categories according to the data structure to account for lack of independence (Gurevitch and Hedges 2001). Effect sizes and variances from each of these (averaged) records were then used to calculate a grand "cumulative" effect size:

$$\overline{\overline{E}} = \frac{\sum w_i Z_i}{\sum w_i} \tag{6}$$

with a standard deviation defined in terms of the weights of the *i* effect sizes, viz:

$$s_{\overline{\overline{E}}} = \sqrt{\frac{1}{\sum w_i}} \tag{7}$$

Using this standard deviation, we constructed lower ($\overline{\overline{E}}^L$) and upper ($\overline{\overline{E}}^U$) 95% confidence limits for the cumulative effect size, respectively, as:

$$\overline{\overline{E}}^L = \overline{\overline{E}} - \left(t_{\alpha/2[n-1]} s_{\overline{\overline{E}}}\right) \tag{8}$$

and

$$\overline{\overline{E}}^U = \overline{\overline{E}} + \left(t_{\alpha/2[n-1]} s_{\overline{\overline{E}}}\right) \tag{9}$$

where $t_{a/2}$ was the 2-tailed critical value of the standard normal distribution (Gurevitch and Hedges 2001). Total heterogeneity in the individual effect sizes in each dataset was estimated as Q_T, which is a measure of the total variation in individual effect sizes (compared to cumulative effect size; Gurevitch and Hedges 2001). Significance of Q_T can be determined by comparing to a c^2 distribution with $N-1$ degrees of freedom, where N is the total number of records used in the analysis. Significance of Q_T indicates that individual effect sizes vary sufficiently and that this variation may be associated with underlying structure in the records. After imposing structure on the dataset, the significance of this structure was assessed by estimating between-class variation in effect sizes, Q_M, and comparing this measure of "among-category" variation to a c^2 distribution with $j-1$ degrees of freedom, where j is the number of categories in the analysis (Gurevitch and Hedges 2001). Significance of Q_M indicates significant among category heterogeneity in effect sizes. This test can be followed by estimation of mean "cumulative" effect sizes within each category ($\overline{E}_j$), their variance ($s^2_{\overline{E}_j}$), and lower ($\overline{E}^L_j$) and upper ($\overline{E}^U_j$) 95% confidence limits in which the critical Type II error rate was adjusted using the Bonferroni method (Rice 1989). All of these analyses were accomplished within a mixed effects mode framework, which assumed that all of the studies in a particular class (e.g., primary producers, detritivores, predators, herbivores, predators, and mixed consumers in the Type of User analysis) shared a common mean effect and thus a common (class-specific) measure of sampling error, but also included random variation among the studies (Gurevitch and Hedges 2001).

Because the mixed effects model uses the pooled residual variance from the fixed effects model as an estimate of the sampling error, we first estimated the pooled residual variance within a fixed effects model framework. The fixed effects model differs from the mixed effects model in that it assumes that all of the studies share a common true effect size and that any differences in the actual effect size among the different studies are due to sampling error (Gurevitch and Hedges 2001). The fixed effects model was implemented using the average effect size (Z_{ij}) and the average weighted effect size (w_{ij}) for each paper in each Type of User, Functional Role, or Ecosystem Type category to calculate the cumulative mean effect size for each Type of User, Functional Role, and Ecosystem Type category as:

$$\overline{E}_j = \frac{\sum_{i=1}^{k_j} w_{ij} Z_{ij}}{\sum_{i=1}^{k_j} w_{ij}} \qquad (10)$$

where k_j was the number of studies in category j (Rosenberg et al. 2000). The standard deviation of $\overline{E}_j$ was:

$$s_{\overline{E}_j} = \sqrt{\frac{1}{\sum_{i=1}^{k_j} w_{ij}}} \tag{11}$$

We calculated the lower ($\overline{E}_j^L$) and upper ($\overline{E}_j^U$) 95% confidence limits for $\overline{E}_j$, respectively, as:

$$\overline{E}_j^L = \overline{E}_j - \left[t_{\alpha/2k} s_{\overline{E}_j}\right] \tag{12}$$

and

$$\overline{E}_j^U = \overline{E}_j + \left[t_{a/2k} s_{\overline{E}_j}\right] \tag{13}$$

As described in the Methods section, $t_{a/2}$ was the two-tailed critical value of the standard normal distribution (Gurevitch and Hedges 2001), adjusted using the Bonferroni correction (Rice 1989) where *k* is the number of categories.

Next we calculated a grand "cumulative" effect size across the Type of User, Functional Role, and Ecosystem Type categories as:

$$\overline{\overline{E}} = \frac{\sum_{i=1}^{m} \sum_{i=1}^{k_j} w_{ij} Z_{ij}}{\sum_{i=1}^{m} \sum_{i=1}^{k_j} w_{ij}} \tag{14}$$

Here, *m* was the total number of categories (*i.e.*, *m* = 5: primary producers, detritivores, herbivores, predators, and mixed consumers). The standard deviation of the grand cumulative effect size was:

$$s_{\overline{\overline{E}}} = \sqrt{\frac{1}{\sum_{i=1}^{m} \sum_{i=1}^{k_j} w_{ij}}} \tag{15}$$

To determine if the effect sizes were significantly different among the Type of User, Functional Role, and Ecosystem Type categories, we calculated a homogeneity statistics Q_T, Q_E, and Q_M. Here total homogeneity, Q_T, included both within-class homogeneity, Q_E, and between-class homogeneity, Q_M.

$$Q_T = Q_M + Q_E \tag{16}$$

Within-class homogeneity, Q_E, a measure of the variation among records within each category, was calculated as:

$$Q_E = \sum_{j=1}^{m} \sum_{i-1}^{k_j} w_{ij} \left(Z_{ij} - \overline{E}_j\right)^2 \tag{17}$$

Between-class homogeneity, Q_M, a measure of the variation between categories in mean effect size (Rosenberg et al. 2000), was calculated as:

$$Q_M = \sum_{j=1}^{m} \sum_{i-1}^{k_j} w_{ij} \left(\bar{E}_j - \bar{\bar{E}} \right)^2 \qquad (18)$$

Once we calculated the fixed effects model, we were able to carry out the mixed effects model using the variance from the fixed effects model to calculate sampling error. As with the fixed effects model, we needed to calculate Z_{ij}, v_{ij}, w_{ij}, w_{ij}^2, $v_{ij}*$, $w_{ij}*$, and $w_{ij}*Z_{ij}$ for each record (the asterisk indicates the mixed model version of the term). Here $v_{ij}*$, $w_{ij}*$, and $w_{ij}*Z_{ij}$ included both the unconditional variance, v_{ij}, and the pooled within class variance, σ^2_{pooled}, which was calculated as:

$$\sigma^2_{pooled} = \frac{Q_E - (n - m)}{\sum_{j=1}^{m} \left(\sum_{i=1}^{n} w_{ij} - \frac{\sum_{i=1}^{k_j} w_{ij}^2}{\sum_{i=1}^{k_j} w_{ij}} \right)} \qquad (19)$$

Here, Q_E was within-class heterogeneity, n was the total number of studies, m was the number of categories, k_j was the number of studies in the j^{th} category, and w_{ij} was the fixed effects weight of the i^{th} study in the j^{th} category. Cumulative effect size for each category, $\bar{E}_j$, and its variance, $s_{\bar{E}_j}$, were calculated as in the fixed effects model (equations 10 and 11). We calculated the grand cumulative effect size, $\bar{\bar{E}}^*$, and its standard deviation, $s_{\bar{\bar{E}}^*}$, as:

$$\bar{\bar{E}}^* = \frac{\sum_{i=1}^{m} w_{ij}^* Z_{ij}^*}{\sum_{i=1}^{m} w_{ij}^*} \qquad (20)$$

and

$$s_{\bar{\bar{E}}^*} = \sqrt{\frac{1}{\sum_{i=1}^{m} \sum_{j=1}^{k_i} w_{ij}^*}} \qquad (21)$$

We then calculated the homogeneity among the categories as:

$$Q_M^* = \sum_{i=1}^{m} w_{ij}^* Z_{ij}^{*2} - \frac{\left(\sum_{i=1}^{m} w_{ij}^* Z_{ij}^*\right)^2}{\sum_{i=1}^{m} w_{ij}^*} \qquad (22)$$

where w_{ij}^* was the sum of the mixed model weights for each category (Gurevitch and Hedges 2001):

$$w_{ij}^* = \frac{1}{\frac{1}{w_{ij}} + \sigma_{pooled}^2} \qquad (23)$$

Mixed model meta-analysis is less frequently performed in ecology than fixed effect analyses, but is typically more conservative (Rosenberg et al. 2000). Generally, an effect size of 0.2 is considered a "small" effect, 0.5 is a "medium" effect, and a magnitude of 0.8 is considered a "large" effect (Cohen 1969).

TABLE 16. Types of detritus used in literature search and associated ecosystem type.

Type of detritus	Ecosystem type
Detritus	Freshwater and terrestrial
Leaf litter	Freshwater and terrestrial
Leaf fall	Freshwater and terrestrial
Mulch	Terrestrial
Tussock litter	Terrestrial
Plant litter	Terrestrial
Large woody debris OR LWD	Freshwater
Snags	Freshwater and terrestrial
Dead wood	Freshwater and terrestrial
Slash	Terrestrial
Coarse particulate organic matter OR CPOM	Freshwater
Fine particulate organic matter OR FPOM	Freshwater
Dissolved organic matter OR DOM	Freshwater and terrestrial
Seston	Freshwater and marine
Nekton	Freshwater and marine
Sea wrack OR wrack	Marine
Plankton rain	Marine
Marine snow	Marine
Carrion	Terrestrial
Guano	Terrestrial
Frass	Terrestrial
Scat	Terrestrial
Dung	Freshwater and terrestrial
Sea grass OR (kelp AND deep sea)	Marine
Glucose	Freshwater, marine, and terrestrial
Dissolved organic carbon OR DOC	Freshwater, marine, and terrestrial
Soil	Terrestrial

TABLE 17. Summary of formulas used to convert test statistics to *R*.

Test statistic	Data required	R conversion
Standardized mean difference	$\overline{X}^{+D}$, $\overline{X}^{-D}$, s^{+D}, s^{-D}, N^{+D}, N^{-D}, d_{ij}	$R = \sqrt{\frac{d_{ij}^2 N_{ij}^{-D} N_{ij}^{+D}}{d_{ij}^2 N_{ij}^{-D} N_{ij}^{+D} + \left(N_{ij}^{-D} + N_{ij}^{+D}\right) + \left(N_{ij}^{-D} + N_{ij}^{+D}\right.}}$
F-statistic[ab]	SS_{effect}, SS_{total}, F	$R = \sqrt{\frac{SS_{effect}}{SS_{total}}}$
R[b]	*R, N*	-
R^2[b]	R^2, N	$R = \sqrt{R^2}$
Spearman *R*[b]	*R, N*	-
t-test[b]	t, N, df_{error}	$R = \sqrt{\frac{t^2}{t^2 + df_{error}}}$

[a] Sign of *R* inferred from direction of linear effects.

[b] This formula applies only to 1-way ANOVA designs. Conversions for 2-way and higher order designs are more complicated; see Levin and Hullett 2002 for details.

Paired measurements of primary producer, detritivore, herbivore, and predator response to detritus

We found 23 records from 10 studies in our meta-analytic database that presented paired measurements of effect size of detritus on detritivores and predators, 11 records from seven studies had complimentary measurements of effect sizes for detritivores and herbivores, and 18 records from 9 studies had paired measurements for herbivores and predators. Ten records from 4 studies had paired measurements of primary producer, herbivore, and predator effect sizes. These few but valuable records allowed us to evaluate the potential for direct and indirect effects of detritus in food webs. Relationships between the unweighted effect size (+/- SD) of these paired studies were examined using Pearson Product Moment Correlations.

RESULTS

Meta-analysis

Detritus had systematic, positive and significant effects on primary producers and consumer standing stocks (abundance, biomass, and density) from diverse ecosystems ($\overline{\overline{E}} = 1.308 \pm 0.177$, grand cumulative effect size ± 95% confidence interval; Table 18). Moreover, variation in effect sizes (E_{ij}) among records in our database was low and non-significant ($Q_M = 6.84$, $df = 4$, $P = 0.1$) further underscoring the systematic positive and significant effects of detritus resulting spite of non-significant total variation in individual effect sizes. We then categorized responses of different Types of Users to detritus and found that detritus had uniformly significant positive effects on primary producers and all higher-level consumer groups (detritivores, herbivores, predators, and mixed consumers; Table 18, Fig. 25). Effect sizes of detritus on richness were not significant overall ($\overline{\overline{E}} = 0.367 \pm 0.441$, grand cumulative effect size ± 95% confidence interval) or for any group of consumers, although sample sizes were very low for predators and herbivores (Table 19). Given the larger sample size and much stronger effects of detritus on standing stocks of consumers, we narrowed our dataset to studies on standing stocks for all subsequent analyses.

Detritus played different functional roles for detritivores, herbivores, and predators in our dataset (Table 20), serving exclusively as habitat for herbivores and predators, but serving as exclusively food (energetic), exclusively habitat, or both for detritivores. Detritus had uniformly positive effects on higher-level consumers in spite of the various functional roles detritus played for these consumer groups (energetic, habitat, or both; Table 20). Specifically, we found no significant variation in the effects of detritus on the standing stock of consumers where it served energetic, habitat, or both (energetic and habitat) roles for these consumers ($Q_M = 7.62$, $df = 4$, $P = 0.1$). The overall effect of detritus on higher-level consumers was positive and significant ($\overline{\overline{E}} = 1.437 \pm 0.245$, grand cumulative effect size ± 95% confidence interval; Table 20, Fig. 26a). Effect sizes of detritus on detritivore standing stocks were significant when detritus served as an energetic resource or both an energetic resource and habitat, but not when detritus served the role of habitat alone (Fig. 26b). Finally, the effect of detritus as habitat on herbivores and predators was also positive and significant (Fig. 26c-d).

Finally, we sub-divided “standing stock” studies into those occurring in aquatic and terrestrial Ecosystem Types and analyzed the effect of Ecosystem Type on the mean effect size. Ecosystem Type had a strong positive effect ($Q_M =$

15.01, *df* = 1, $P < 0.001$), with detritus having a stronger positive effect in terrestrial than aquatic ecosystems ($\overline{\overline{E}} = 0.972 \pm 0.317$ and $\overline{\overline{E}} = 1.632 \pm 0.299$, grand cumulative effect size ± 95% confidence interval for aquatic and terrestrial ecosystem types, respectively; Fig. 27).

Fail-safe estimates were quite high for all analyses. Fail-safe numbers for the effect of detritus on primary producers and consumer standing stocks, the effect of detritus on consumers when classified by functional role, the effect of detritus in aquatic versus terrestrial ecosystem types were all > 1,000. Thus, the file drawer problem was likely not an issue in this study.

TABLE 18. Results of mixed effects model for effects of detritus on primary producers and detritivore, herbivore, predator, and mixed consumer standing stocks.

Type of user	Effect size	Variance	Lower 95% CL	Upper 95% CL
Cumulative effect size				
Primary producers	1.572	0.041	0.960	2.183
Detritivores	1.408	0.015	1.056	1.761
Herbivores	1.044	0.054	0.311	1.778
Predators	1.303	0.032	0.765	1.842
Mixed consumers	0.928	0.046	0.264	1.592
Grand cumulative effect size	1.308	0.006	1.131	1.485

Notes: Standing stocks include abundance, biomass, or density. CL is confidence limit.

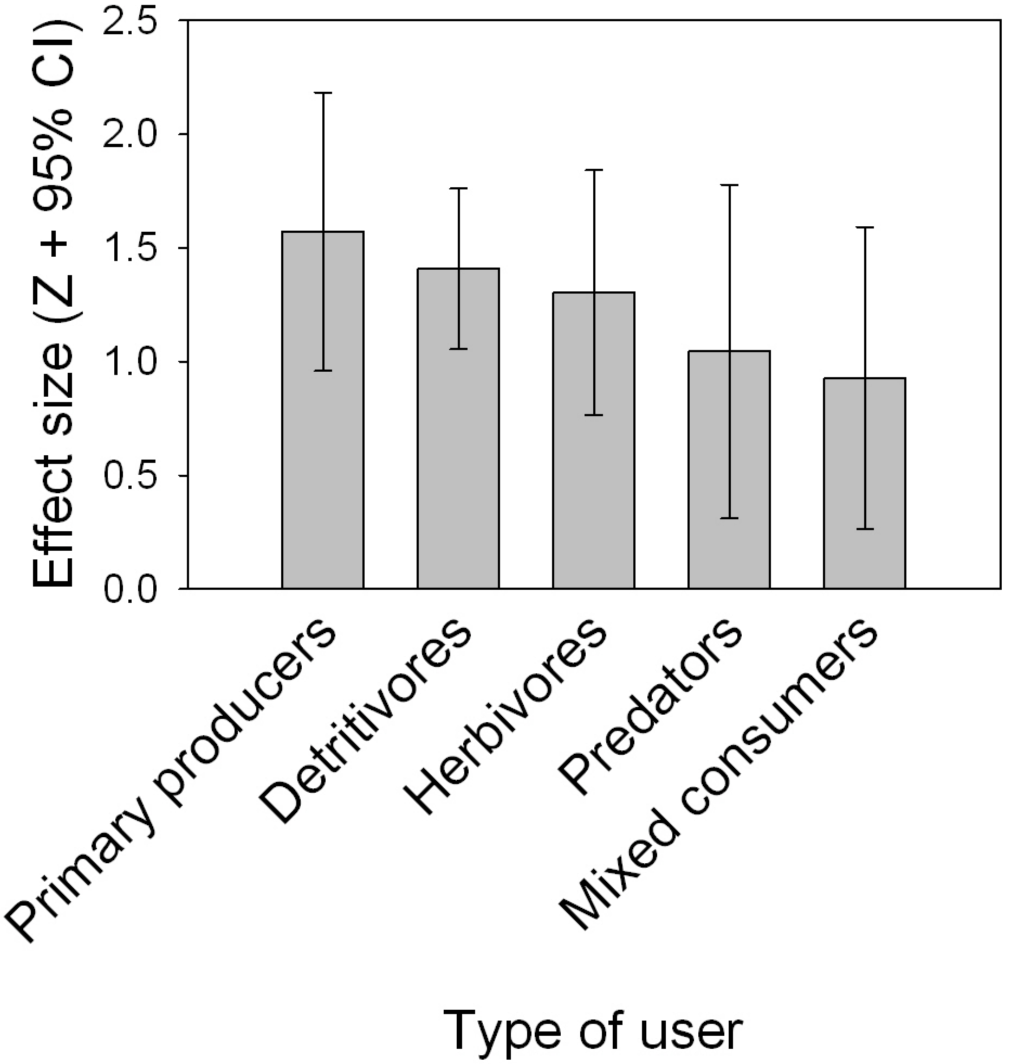

FIG. 25. Cumulative effect size of detritus on primary producer and consumer standing stocks. Sample sizes are primary producers = 30, detritivores = 75, herbivores = 21, predators = 35, and mixed consumers = 24.

TABLE 19. Cumulative and grand cumulative effect size of detritus on the consumer richness.

Type of consumer	Effect size	Variance	Lower 95% CI	Upper 95% CI
Cumulative effect size				
Detritivore	0.456	0.086	-0.416	1.327
Predator	0.529	0.184	-2.133	3.191
Herbivore	-1.551	0.545	-	-
Mixed	0.499	0.082	-0.315	1.312
Grand cumulative effect size	0.367	0.032	-0.074	0.808

Notes: Sample sizes are detritivores = 7, herbivores = 1, predators = 3, and mixed consumers = 8.

TABLE 20. Results of mixed effects models for functional role of detritus on all consumers pooled and for individual consumer groups.

Functional role	Effect size	Variance	Lower 95% CL	Upper 95% CL
All consumers				
Cumulative effect size				
Energetic	1.755	0.020	1.428	2.083
Habitat	1.178	0.019	0.858	1.499
Both	1.240	0.020	0.915	1.565
Grand cumulative effect size	1.387	0.006	1.205	1.570
Individual consumers groups				
Cumulative effect size				
Detritivores - Energetic	1.861	0.039	1.276	2.4467
Detritivores - Habitat	1.596	0.203	-0.218	3.410
Detritivores - Both	1.258	0.047	0.608	1.908
Herbivores - Habitat	1.052	0.083	0.143	1.961
Predators - Habitat	1.296	0.050	0.592	1.999
Grand cumulative effect size	1.437	0.012	1.192	1.681

Notes: Pooled consumers include detritivores, predators, herbivores, and mixed consumers. The functional role of detritus for detritivores was energetic, habitat, or both, while the functional role of detritus for herbivores and predators was only habitat. CL is confidence limit.

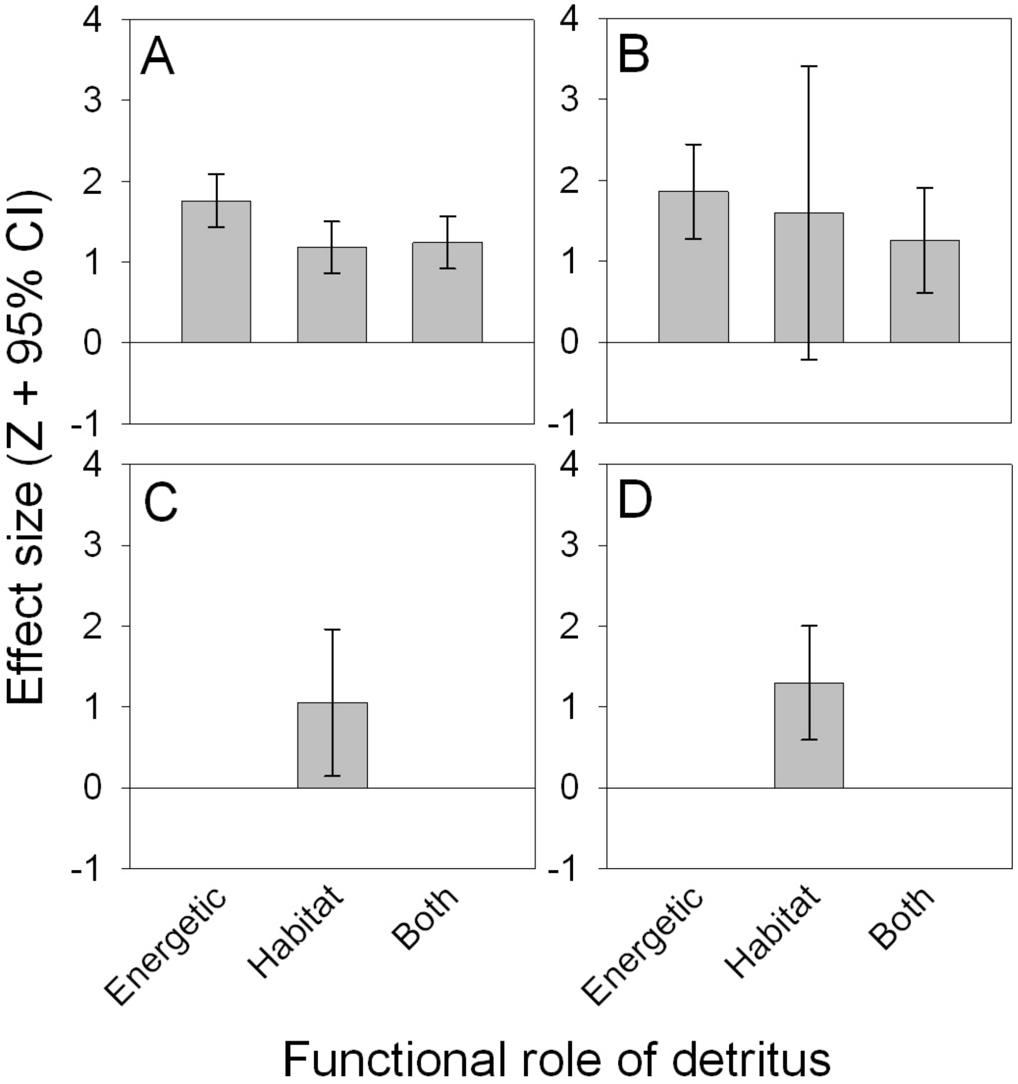

FIG. 26. Cumulative effect size of detritus on all consumers pooled (detritivores, predators, herbivores, and mixed consumers; A), detritivore (B), herbivore (C), and predator (D) standing stocks when the primary effects of detritus on a target group of consumers were classified a priori by authors as either energetic, habitat, or both (energetic and habitat). Sample sizes for all consumers are energetic = 44, habitat = 45, and both = 44; detritivores are energetic = 42, habitat = 8, and both = 35; herbivores is habitat = 21; and predators is habitat = 21. B and C do not include bars for “Energetic” or “Both” because detritus only provides habitat for herbivores and predators.

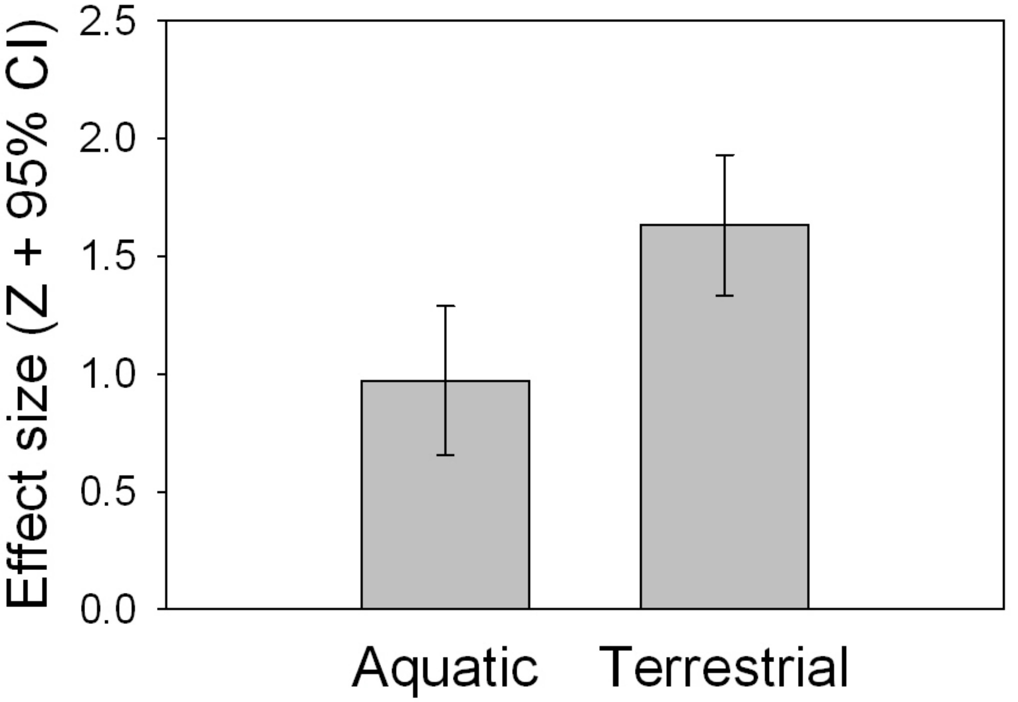

FIG. 27. Cumulative effect size of detritus on primary producer and consumer standing stocks in aquatic and terrestrial ecosystems. Sample sizes for aquatic ecosystems is 74 and terrestrial ecosystems is 86.

Effects of detritus on green channel trophic dynamics

Effect sizes for detritivores were positively related to those of predators in the 23-paired studies in our database ($r = 0.58$, $P < 0.01$; Fig. 28a). Effect sizes of herbivores were not significantly correlated with those for either predators ($r = -0.1$, $P = 0.68$; Fig. 4b) or detritivores ($r = -0.08$, $P = 0.81$; data not shown). Effect sizes of primary producers were positively, but only marginally related to those of herbivores ($r = 0.61$, $P < 0.06$; Fig. 28c). Finally, effect sizes of predators and primary producers were negatively correlated in the 10-paired studies in our database ($r = -0.79$, $P < 0.01$; Fig 28b).

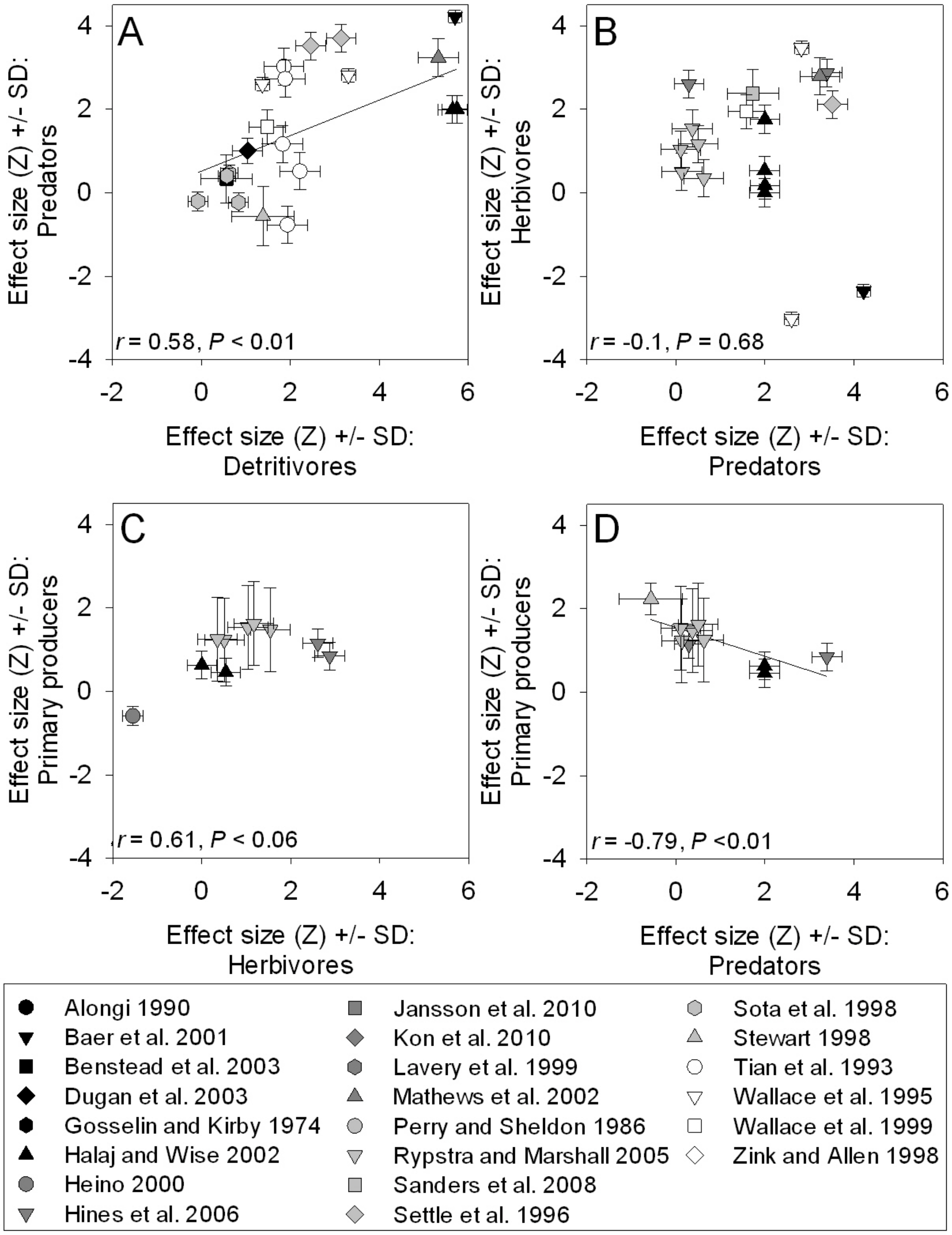

FIG. 28. 23 records from 11 studies that had paired measurements of detritivore and predator responses to detritus (A), 18 records from 9 studies that had paired measurements of herbivores and predators (B), 10 records from 4 studies that had paired measurements of primary producer and herbivore responses to detritus (C), and 10 records from 4 studies that had paired measurements of primary producers and predators (D). Types of detritus include leaf litter, large woody debris in streams, sea wrack, seston, insect carcasses in pitcher plants, shell fields in lakes, mulch and compost on agricultural fields, and thatch in intertidal zones. Data show unweighted effect sizes and SD of these.

DISCUSSION

Detritus is a prominent fixture in classic food web descriptions (Lindeman 1942, Odum 1957, Minshall 1967), and a focal point of debate in current theories about the role of top down forces in food chains (Hairston and Hairston 1993, Polis and Strong 1996, Akin and Winemiller 2006, Yuma et al. 2006, Attayde and Ripa 2008). In this paper we show that detritus fuels the food web from the bottom up, having consistently strong positive effects at all trophic levels in a variety of ecosystem types. Effect sizes of detritus are significant and positive for primary producers, detritivores, herbivores, and predators, and detritus has similar positive effects on a variety of consumers in both aquatic and terrestrial ecosystem types. Detritus has a direct positive effect on detritivores by providing an energetic resource and both an energetic resource and habitat (refuge from predators). Detritus also has a direct positive effect on herbivores and predators by providing a source of habitat for these animals. Detritus has significantly stronger effects on plants and consumers in terrestrial versus aquatic ecosystems, though mean effect sizes are significantly greater than zero (positive) in both ecosystem types. Finally, we find more support for the notion that detritus determines trophic structure in the green channel via fertilization of primary producers (bottom-up control) than by catalyzing strong effects of subsidized predators on herbivores (top-down control mediated by detritus).

Diverse functional roles of detritus

Results of our meta-analysis suggest that the effects of detritus reach much further than the expected contribution of energetic and habitat resources to detritivores. In particular, detritus provides herbivores and predators with an important habitat resource. For example, large woody debris creates pool habitat for herbaceous insects (Wallace et al. 1995), predatory insects (Wallace et al. 1995), and fish (Warren and Kraft 2003) in headwater streams. Detritus in the form of mulch, compost, and till provide structure for herbaceous insects (Rypstra and Marshall 2005), spiders (Halaj et al. 2000, Halaj and Wise 2002), ants (Tian et al. 1993), and other insect predators (Rypstra and Marshall 2005) in agricultural ecosystems. A strong correlation between the effect sizes detritivores and predators suggests that detritus provides an important indirect energetic resource to predators as well. Here, strong bottom-up effects of detritus on predators are mediated by increased detritivore prey abundance or biomass. We find that detritus provides an important energetic resource to predators in a wide variety of habitats, including streams (Wallace et al. 1995, Wallace et al. 1999, Baer et al. 2001, Benstead et al. 2003), beaches (Dugan et al. 2003), lakes (Stewart et al. 1998), intertidal salt marsh (Hines et al. 2006), tree holes (Sota et al. 1998), agricultural fields (Settle et al. 1996, Halaj et al. 2000, Halaj and Wise 2002), and apple orchards (Mathews et al. 2002). Not only does detritus provide significant structural habitat to predators in a wide variety of ecosystems, it offers an essential energetic resource for these consumers as well.

Detritus is important in diverse ecosystems

Detritus has similar strong positive effects on a variety of consumers in a diverse range of ecosystem types. While numerous papers have examined the role of detritus on consumer populations, there have been few attempts to compare the effects of detritus across multiple ecosystem types. Here we find that detritus has strong general effects on consumer standing stocks in a wide range of ecosystem types including, but not limited to: soil food webs, streams, lakes, beaches, the water column in the open ocean, and the deep sea floor. Records included in our meta-analysis generally fell into two ecosystem types: aquatic (marine and freshwater) and terrestrial. Detritus has consistent significant and positive effects on consumer standing stocks in both ecosystem types, but has significantly stronger effects on consumers in terrestrial systems. Thus our data are consistent with previous work suggesting differences in the structure and function of food webs in aquatic and terrestrial systems—terrestrial food webs respond more strongly to inputs of detritus than do aquatic food webs.

Effects of detritus on trophic structure in the green channel of the food web

Detrital resources were expected to have positive bottom up effects on consumers (DeAngelis 1992, Polis and Hurd 1996). However, we also find that detritus has significant positive effects on primary producers, providing support for a "fertilization effect" of detritus on plant productivity. Detritus has bottom-up effects on primary producers by altering nutrient supply, light levels, and secondary compounds. For example, manure and vegetable compost provide essential nutrients that support plant production (Rypstra and Marshall 2005, Tittarelli et al. 2009). In our meta-analysis, we examined how a combination of variables, including plant biomass, height, and number of leaves responded to detrital resources. As expected, the majority of studies showed a positive effect of detritus on primary producers. The few studies that had a negative effect include sediment organic-C reducing ciliate and flagellate chlorophyll *a* concentrations in the deep sea (Alongi 1990), CPOM reducing moss and macrophyte cover in a lake ecosystem (Heino 2000), and woody debris slash reducing herbaceous and woody plant biomass in a temperate forest (Krueger and Peterson 2009). These negative effects of detritus on primary producers primarily result from detritus reducing light availability.

Our meta-analysis shows that detritus has strong positive effects on herbivore standing stocks. Positive effects of detritus on herbivores could arise from three very different mechanisms. First, some herbivores may exhibit some omnivory (Polis and Strong 1996). For example, many presumed stream herbivores may consume biofilms and other forms of fine particulate detrital organic matter (Mulholland et al. 2000). Second, positive effects of herbivores to detrital resources could result from top predators switching from herbivore to detritivore prey (Halaj and Wise 2002). Variable amounts of detrital resources have been shown to influence food web interactions (Polis and Strong 1996, Huxel and McCann 1998). Finally, detritus may have an indirect positive effect on herbivores via fertilization of primary producers. Effect sizes of primary producers are positively related to those of herbivores. This correlation is strong but only marginally significant, likely due to small sample size ($N = 10$). A strong correlation between effect sizes of plants and herbivores coupled with the observation that detritus has a significant positive effect on primary producers suggests strong bottom-up control of the green channel. This observation is strengthened by the large positive effect size of detritus on predators and positively correlated effect sizes of detritivores and predators. In addition to its role as the resource base for detritivores, detritus influences the standing stocks of primary producers, herbivores, and predators.

We did not find significant correlations between effect sizes for herbivores and those for either predators or detritivores (though both correlations were weakly negative). Thus, the effects of detritus appear not to catalyze negative indirect effects of predators on herbivores by virtue of enhancing detritivore abundance or biomass. Interestingly, the effect sizes for herbivores and predators are almost all positive. This likely results from predators switching to detrital based resources when they are available thus releasing herbivores from predation during short-term experiments. Further, high variability in relationships among detritivores, herbivores, and predators suggests system-specific attributes (e.g., size, quality, or functional role of detritus) may determine whether detritus promotes or precludes cascades in the green channel. Thus our results point to strong bottom-up control of detritus at all higher trophic levels, with weak at best support for detrital mediated trophic cascades in the green channel.

Green world theory holds that predators limit the abundance of herbivores, allowing for accumulation of living plant biomass (Hairston et al. 1960, Hairston and Hairston 1993). Predators elicit trophic cascades (Carpenter and Kitchell 1988), whereby they have indirect positive effects on plants by virtue of their strong effects on herbivores. Detritus is generally ignored in classic green world theories of trophic structure (Oksanen et al. 1981) and in even the most elegant tests of these theories (Pace et al. 1999). By contrast, an alternate viewpoint of food web dynamics suggest that detritus behaves in ways similar to net primary production (as a bottom up resource), despite its representation in models as a donor-controlled (brown world) resource (Allison 2006). Our results support the notion that detritus has strong bottom-up effects on higher trophic levels, as well as a significant fertilization effect on the green channel.

Conclusion

In this paper we show that detritus has strong effects on the abundance, biomass, and density of detritivores in a broad range of ecosystems across the globe. Further, we show that detritus has nearly equally strong effects on herbivores and predators of these consumers. Strong effects of detritus on predators arise through both direct (detritus provides structural habitat for these consumers higher in the food chain) and indirect channels (energy flow from detritus through detritivores). Our results also suggest that detritus has positive effects on consumers in both aquatic and terrestrial ecosystems, but stronger effects on consumers in terrestrial food webs. Finally, we show that detritus has a strong fertilization effect on primary producers in a variety of ecosystem types. Thus, detritus shapes food web structure via multiple direct and indirect pathways suggesting that it is an integral component of the trophic dynamics in ‘living’ or ‘green channels’ in a wide variety of food webs. Finally, our results suggest that future studies of detritus should measure the collective response of whole communities—plants, detritivores, herbivores, and predators, alike—so that we can reach a better consensus on the role of detritus on food web dynamics.

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APPENDIX C

SUPPLEMENTARY MATERIAL FOR A LANDSCAPE PERSPECTIVE ON BAT FORAGING ECOLOGY ALONG RIVERS: DOES CHANNEL CONFINEMENT AND INSECT AVAILABILITY INFLUENCE THE RESPONSE OF BATS TO AQUATIC RESOURCES IN RIVERINE LANDSCAPES?

BAT CAPTURE DATA

To determine species presence, we captured bats using mist-nets (9 X 2.6m and 18 X 2.6 m nets, 38 mm mesh; Avinet, Inc., Dryden, New York, USA) 9 times along the South Fork Eel River from 24 May – 8 August 2006. We captured 39 bats along the South Fork Eel River, during 9 nights and a total of 23.8 mist–net hours. Five species of bats were captured including 6 *Myotis californicus,* 3 *M. lucifugus,* 4 *M. thysanodes,* 25 *M. yumanensis,* and 1 *Eptesicus fuscus* (TABLE 21).

TABLE 21. Bat species captured along the South Fork Eel River.

Date	Site type	Site name	*Myotis yumanensis*	*Myotis californicus*	*Myotis thysanodes*	*Myotis lucifugus*	*Eptesicus fuscus*	No. bats captured per night	Bat capture rate (no. m^{-2} hr^{-1})
24 May 2006	Unconfined with no alder	Janes	0	0	0	0	0	0	0.000
25 May 2006	Unconfined with alder	Janes	1	1	0	0	0	2	0.005
28 June 2006	Unconfined with alder	Walker Meadow	4	1	1	0	0	6	0.011
29 June 2006	Confined	Wilderness Lodge	2	1	0	0	0	3	0.007
1 July 2006	Unconfined with no alder	White House	5	0	0	0	0	5	0.009
2 July 2006	Unconfined with no alder	Elder	1	0	1	0	0	2	0.006
6 August 2006	Confined	Janes	1	2	1	1	1	6	0.012
7 August 2006	Unconfined with no alder	Merganser	7	1	1	2	0	11	0.012
8 August 2006	Confined	Elder	4	0	0	0	0	4	0.008
Total			25	6	4	3	1	39	

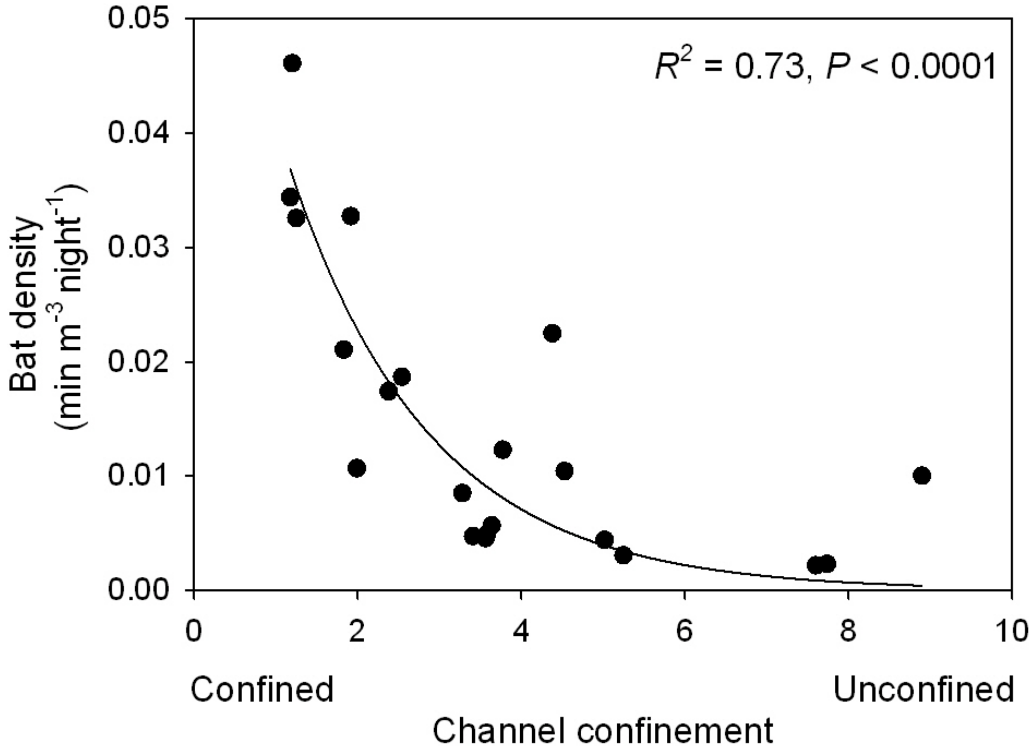


FIG. 29. Mean bat density versus channel confinement. Channel confinement was measured as the ratio of valley floor width (m) to channel width (m). Channel confinement significantly decreases along the X-axis.

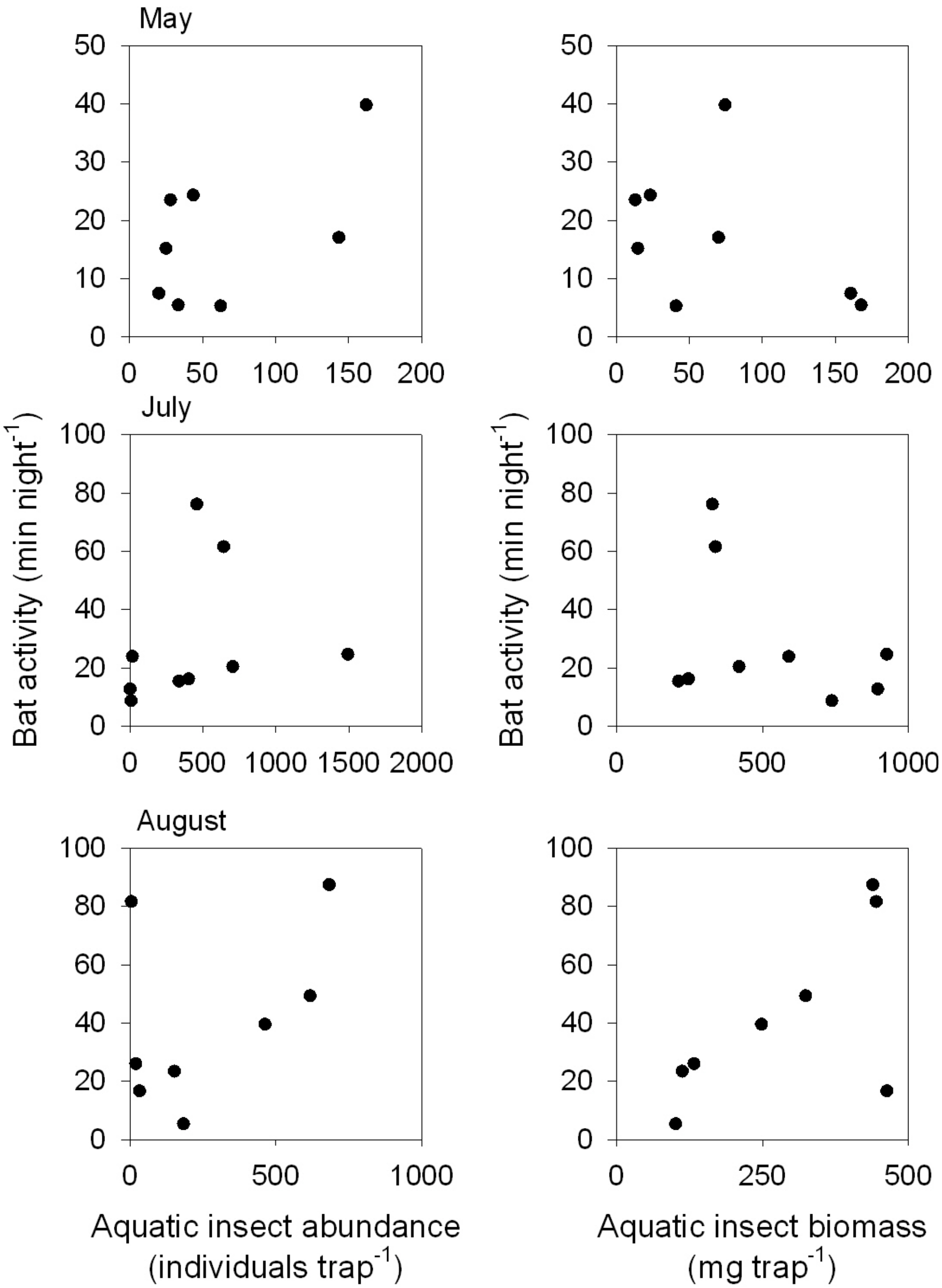


FIG. 30. Mean bat activity versus aquatic insect abundance (left panel) and biomass (right panel) directly above the river in May (top row), July (middle row), and August (bottom row). Notice different scales.

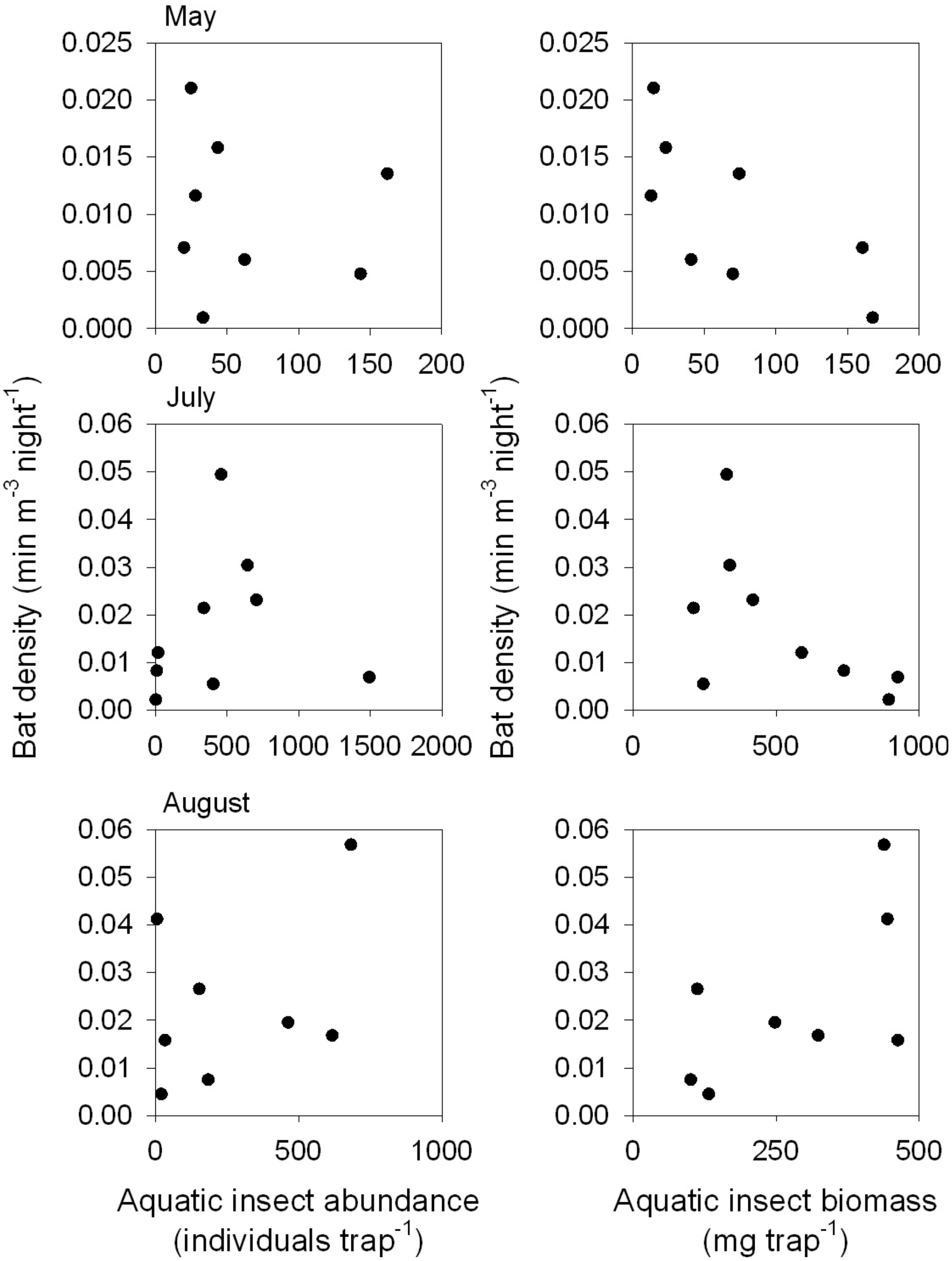


FIG. 31. Mean bat density versus aquatic insect abundance (left panel) and biomass (right panel) directly above the river in May (top row), July (middle row), and August (bottom row). Notice different scales.

TABLE 22. Results of RM ANOVA for bat activity and bat density.

Source of Variation	*df* num	*df* den	*F*	*P*
Bat activity				
(Intercept)	1	10	1492.477	< 0.0001
Site type	2	6	33.607	0.001
Sampling period	2	10	2.738	0.113
Site type: Sampling period	4	10	0.434	0.782
Bat density				
(Intercept)	1	10	1140.917	< 0.0001
Site type	2	6	4.837	0.056
Sampling period	2	10	2.779	0.110
Site type: Sampling period	4	10	0.477	0.752

Notes: Data were ln transformed to meet assumptions of RM ANOVA.

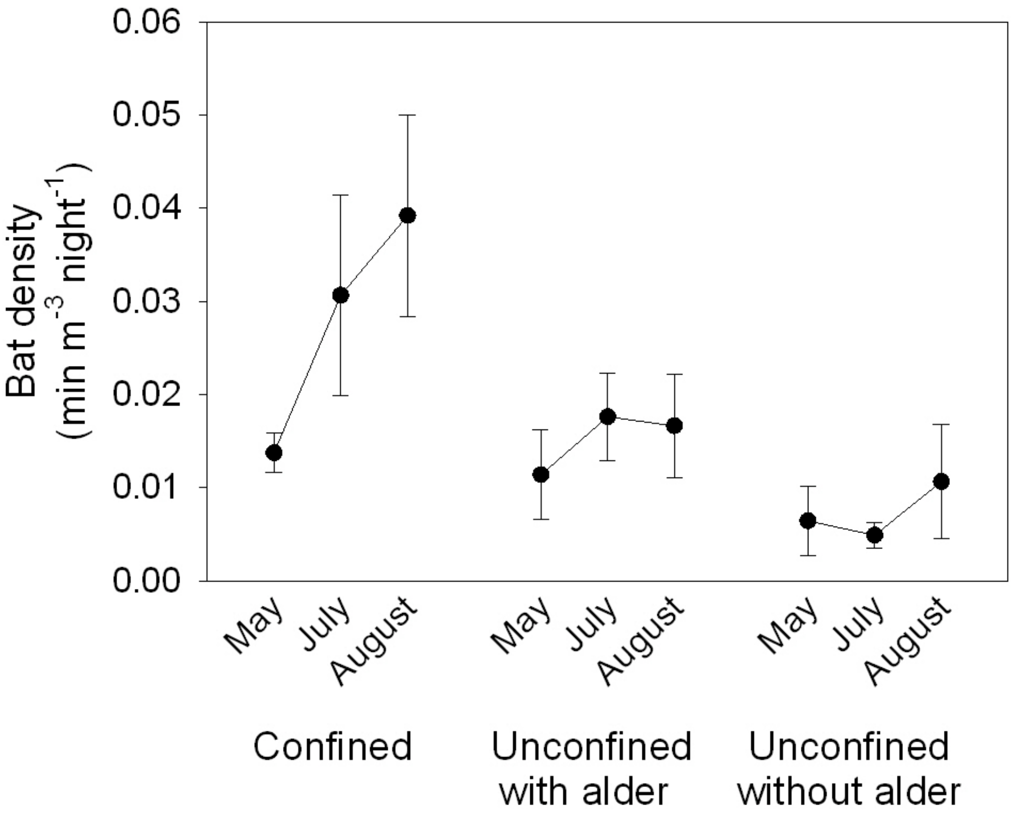


FIG. 32. Mean (± SE) bat density directly above the river at each site type.

TABLE 23. Results of RM ANOVA for aquatic insect emergence, and aquatic and terrestrial insect abundance and biomass.

Source of variation	SS	*df*	MS	*F*	*P*
Aquatic insect emergence rate[a]					
Site type	0.461	2	0.230	1.079	0.422
Error (Site type)	0.854	4	0.214		
Sampling period	42.763	3	14.254	10.745	0.008
Error (Sampling period)	7.960	6	1.327		
Site type x Sampling period	0.990	6	0.165	0.269	0.941
Error (Site type x sampling period)	7.362	12	0.613		
Aquatic insect abundance[ab]					
Site type	0.653	1.000	0.653	0.529	0.543
Error (Site type)	2.472	2.001	1.236		
Sampling period	6.504	1.081	6.019	0.931	0.440
Error (Sampling period)	13.974	2.161	6.465		
Site type x Sampling period	2.718	4.000	0.679	0.936	0.490
Error (Site type x sampling period)	5.808	8.000	0.726		
Terrestrial insect abundance[c]					
Site type	00.379	2	0.189	0.158	0.859
Error (Site type)	4.796	4	1.199		
Sampling period	12.770	2	6.385	3.606	0.127
Error (Sampling period)	7.083	4	1.771		
Site type x Sampling period	4.924	4	1.231	1.899	0.204
Error (Site type x sampling period)	5.186	8	0.648		
Aquatic insect biomass[a]					
Site type	0.795	2	0.397	0.965	0.455
Error (Site type)	1.647	4	0.412		
Sampling period	24.959	2	12.479	45.903	0.002
Error (Sampling period)	1.087	4	0.272		
Site type x Sampling period	3.916	4	0.979	4.894	0.027
Error (Site type x sampling period)	1.600	8	0.200		
Terrestrial insect biomass[c]					
Site type	10.949	2	5.475	3.873	0.116
Error (Site type)	5.654	4	1.414		
Sampling period	24.141	2	12.070	6.321	0.058
Error (Sampling period)	7.638	4	1.910		
Site type x Sampling period	14.924	4	3.731	1.817	0.219
Error (Site type x sampling period)	16.428	8	2.054		

[a] ln transformed.

[b] Sphericity violated, used Huynh and Feldt correction.

[c] ln +1 transformed.

TABLE 24. Results of ANCOVA for aquatic and terrestrial insect abundance and biomass in July.

Source of variation	SS	*df*	MS	*F*	*P*
Aquatic insect abundance					
Corrected Model	14.141	2	7.070	6.208	0.003
Intercept	195.674	1	195.674	171.803	0.000
Distance	13.286	1	13.286	11.665	0.001
Site type	.855	1	0.855	0.750	0.389
Error	78.587	69	1.139		
Total	1536.495	72			
Corrected Total	92.728	71			
Terrestrial insect abundance					
Corrected Model	0.320	2	0.160	0.323	0.725
Intercept	142.590	1	142.590	288.159	0.000
Distance	0.204	1	0.204	0.412	0.523
Site type	0.129	1	0.129	0.261	0.611
Error	33.648	68	0.495		
Total	1047.077	71			
Corrected Total	33.969	70			
Aquatic insect biomass					
Corrected Model	5.160	2	2.580	3.284	0.044
Intercept	237.017	1	237.017	301.679	0.000
Distance	3.483	1	3.483	4.434	0.039
Site type	1.687	1	1.687	2.147	0.147
Error	53.425	68	0.786		
Total	1989.224	71			
Corrected Total	58.585	70			
Terrestrial insect biomass					
Corrected Model	.845	2	0.422	1.080	0.345
Intercept	189.394	1	189.394	484.313	0.000
Distance	.816	1	0.816	2.086	0.153
Site type	.029	1	0.029	0.075	0.785
Error	26.983	69	0.391		
Total	1475.672	72			
Corrected Total	27.828	71			

Notes: Data were ln transformed to meet assumptions of ANCOVA.

TABLE 25. Results of ANCOVA for aquatic and terrestrial insect abundance and biomass in May.

Source	SS	*df*	MS	*F*	*P*
Aquatic insect abundance					
Corrected Model	2.542	2	1.271	1.237	0.296
Intercept	71.250	1	71.250	69.366	0.000
Distance	.009	1	0.009	0.009	0.927
Site type	2.533	1	2.533	2.466	0.121
Error	70.874	69	1.027		
Total	803.281	72			
Corrected Total	73.416	71			
Terrestrial insect abundance					
Corrected Model	.190	2	0.095	0.040	0.961
Intercept	61.640	1	61.640	25.608	0.000
Distance	.177	1	0.177	0.074	0.787
Site type	.005	1	0.005	0.002	0.965
Error	134.795	56	2.407		
Total	565.524	59			
Corrected Total	134.986	58			
Aquatic insect biomass					
Corrected Model	5.992	2	2.996	4.920	0.010
Intercept	99.323	1	99.323	163.104	0.000
Distance	5.548	1	5.548	9.110	0.004
Site type	.444	1	0.444	0.729	0.396
Error	40.800	67	0.609		
Total	799.518	70			
Corrected Total	46.792	69			
Terrestrial insect biomass					
Corrected Model	7.262	2	3.631	1.242	0.296
Intercept	98.209	1	98.209	33.594	0.000
Distance	2.032	1	2.032	0.695	0.408
Site type	4.615	1	4.615	1.579	0.214
Error	166.633	57	2.923		
Total	586.293	60			
Corrected Total	173.895	59			

Notes: Data were ln transformed to meet assumptions of ANCOVA.

TABLE 26. Results of ANCOVA for aquatic and terrestrial insect abundance and biomass in August.

Source	SS	df	MS	*F*	*P*
Aquatic insect abundance					
Corrected Model	8.418	2	4.209	2.393	0.099
Intercept	112.968	1	112.968	64.218	0.000
Distance	7.933	1	7.933	4.510	0.038
Site type	0.707	1	0.707	0.402	0.528
Error	114.345	65	1.759		
Total	786.622	68			
Corrected Total	122.763	67			
Terrestrial insect abundance					
Corrected Model	.793	2	.396	.402	.671
Intercept	82.028	1	82.028	83.164	.000
Distance	.414	1	.414	.420	.519
Site type	.355	1	.355	.360	.551
Error	62.140	63	.986		
Total	767.506	66			
Corrected Total	62.933	65			
Aquatic insect biomass					
Corrected Model	35.981	2	17.991	20.812	.000
Intercept	119.144	1	119.144	137.830	.000
Distance	35.924	1	35.924	41.558	.000
Site type	.014	1	.014	.016	.899
Error	57.052	66	.864		
Total	756.475	69			
Corrected Total	93.034	68			
Terrestrial insect biomass					
Corrected Model	5.484	2	2.742	1.294	.282
Intercept	93.787	1	93.787	44.259	.000
Distance	4.003	1	4.003	1.889	.174
Site type	1.733	1	1.733	.818	.369
Error	127.144	60	2.119		
Total	741.492	63			
Corrected Total	132.627	62			

Notes: Data were ln transformed to meet assumptions of ANCOVA.

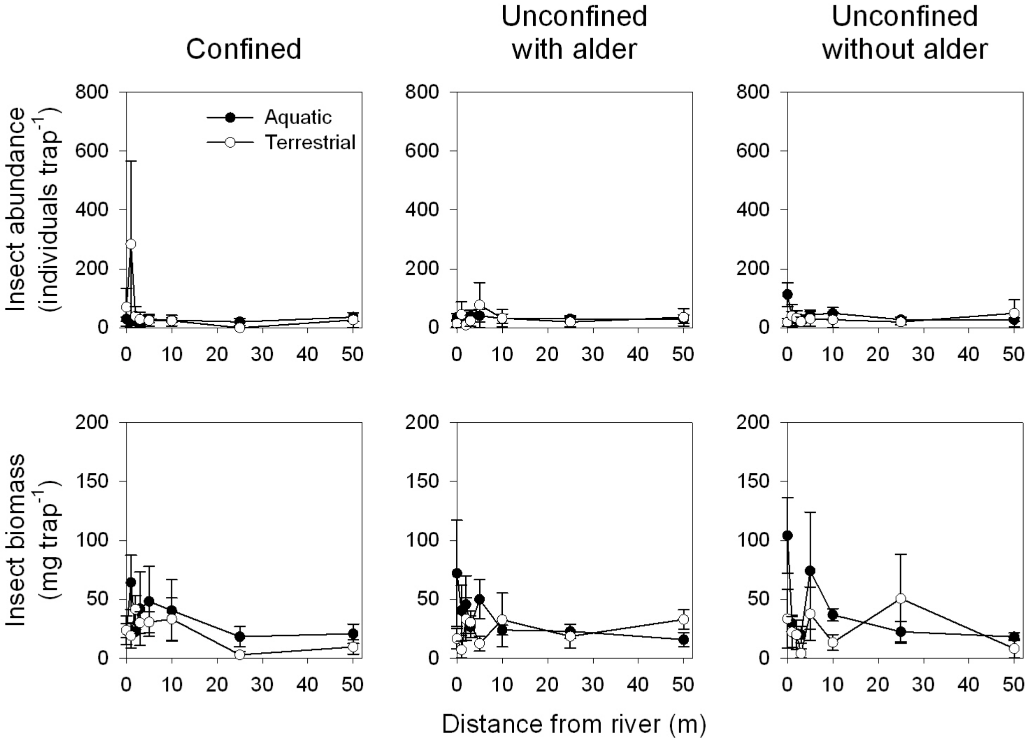


FIG. 33. Mean (± SE) aquatic (closed circles) and terrestrial (open circles) insect abundance (top) and biomass (bottom) with distance from the river at each site type. Samples were collected during a 5-day sampling period in May. Aquatic and terrestrial insect abundance did not vary with distance from river or site type. Aquatic insect biomass was significantly related to distance (ANCOVA, distance treatment effect, ln transformed, $F_{1,67} = 9.1$, $P = 0.004$ but not site type. Terrestrial insect biomass was not related to site type or distance from river.

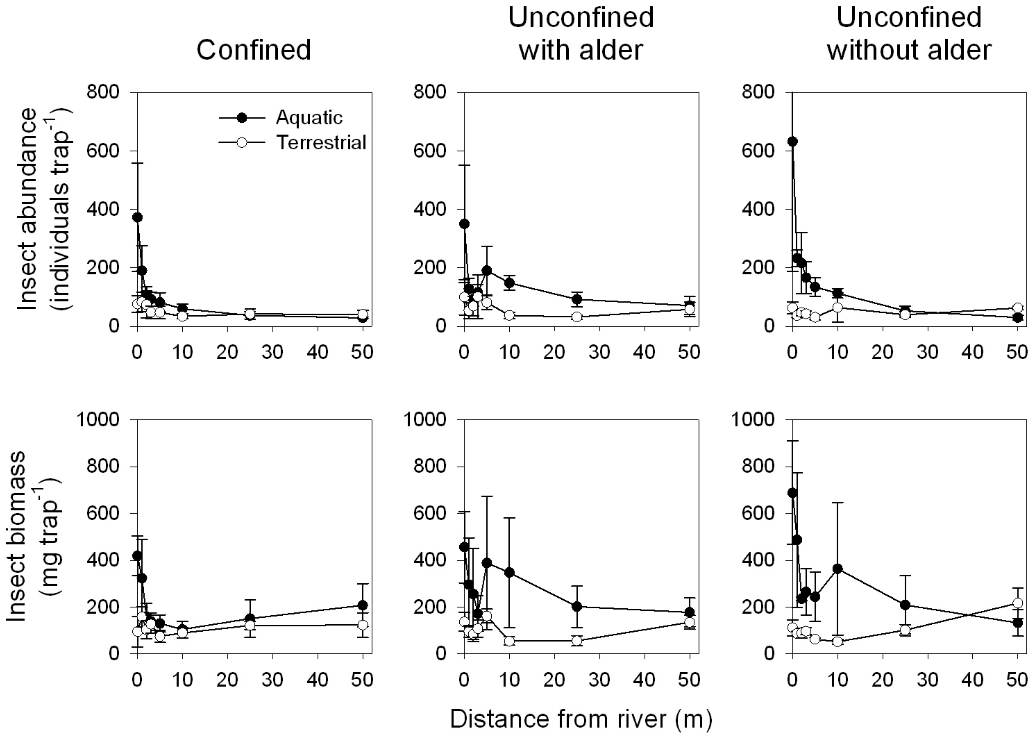


FIG. 34. Mean (± SE) aquatic (closed circles) and terrestrial (open circles) insect abundance (top) and biomass (bottom) with distance from the river at each site type. Samples were collected during a 5-day sampling period in July. Aquatic insect abundance and biomass declined significantly with distance from the river (ANCOVA, distance treatment effect, abundance: $F = 11.7$, df = 1, $P = 0.001$, biomass: $F = 4.4$, $df = 1$, $P = 0.04$) but did not vary with site type. Terrestrial insect abundance or biomass was not related to site type or distance from river.

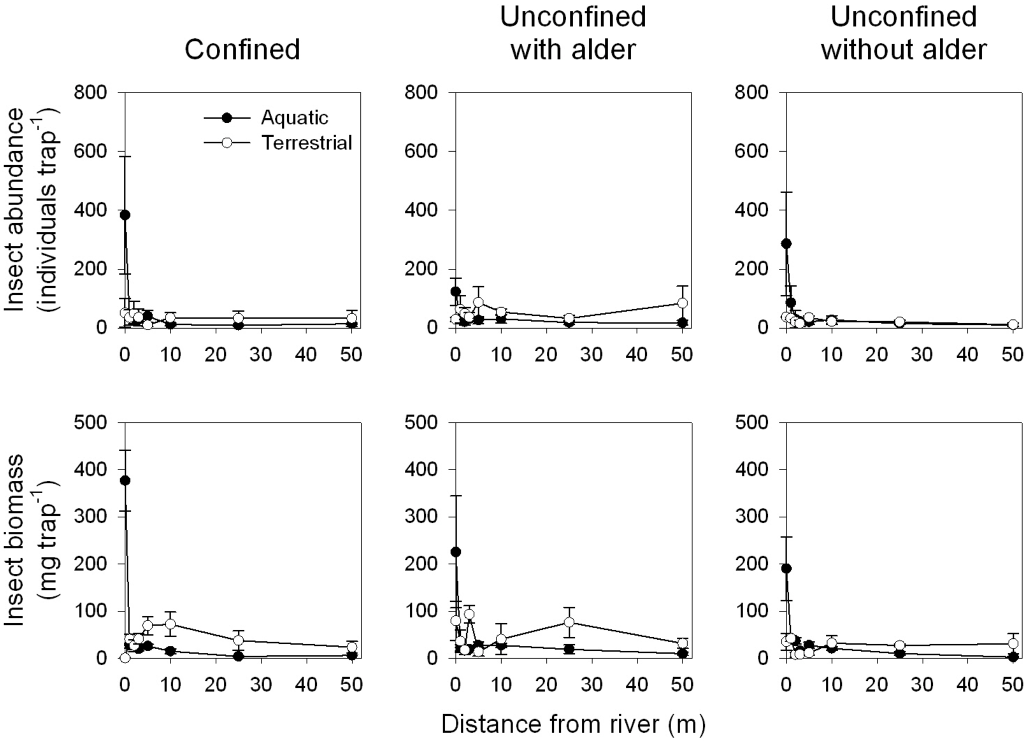


FIG. 35. Mean (± SE) aquatic (closed circles) and terrestrial (open circles) insect abundance (top) and biomass (bottom) with distance from the river at each site type. Samples were collected during a 5-day sampling period in August. Aquatic insect abundance vary with distance from river (ANCOVA, distance treatment effect, ln transformed, $F_{1,65} = 4.5$, $P = 0.04$) but not site type. Terrestrial insect abundance was not related to distance or site type. Aquatic insect biomass was significantly related to distance (ANCOVA, distance treatment effect, ln transformed, $F_{1,69} = 41.6$, $P < 0.001$) but not site type. Terrestrial insect biomass was not related to site type or distance from river.

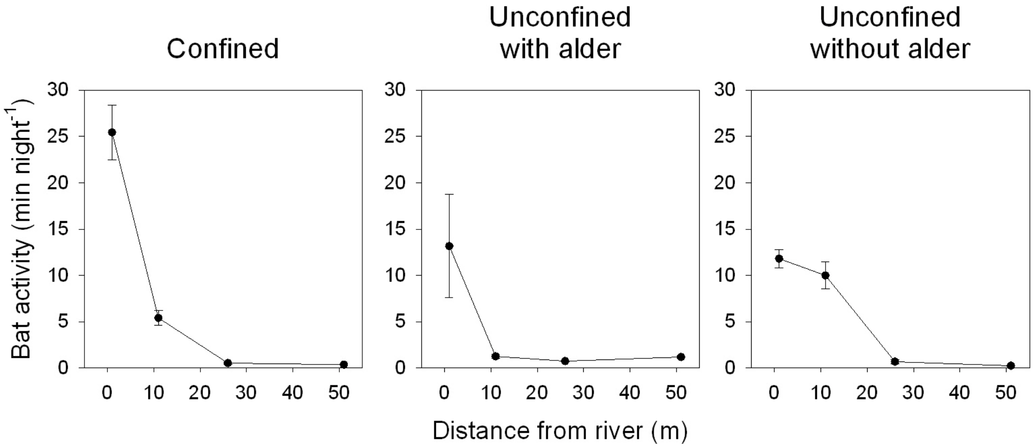


FIG. 36. Mean (± 1 SE) minutes of bat activity per night with distance from the river at each site type. Bat activity measurements coincide with July insect sampling period. Error bars represent error in time (3 consecutive nights) decay not space.

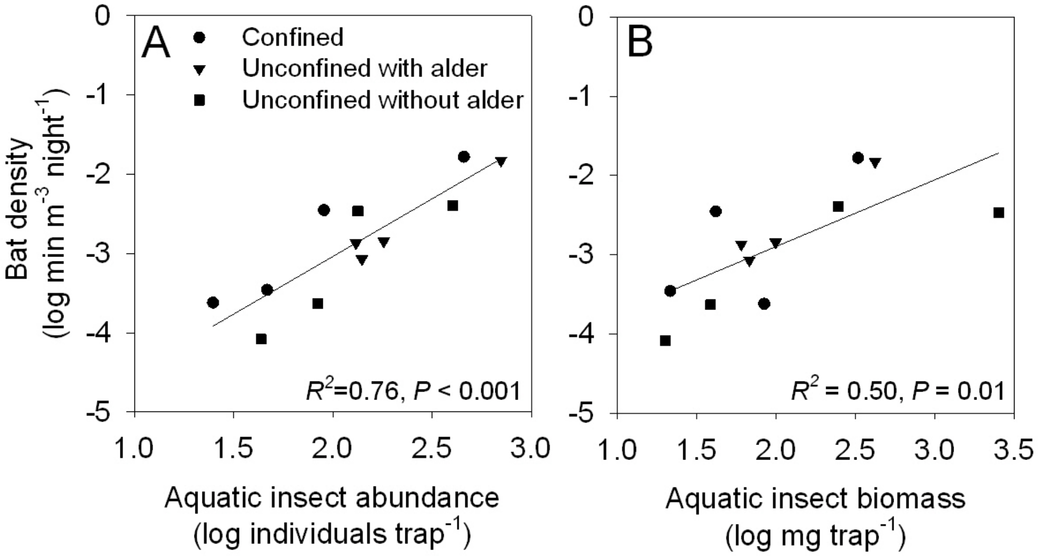


FIG. 37. Mean bat density versus aquatic insect abundance (A) and biomass (B) with lateral distance from the river at each site type during peak insect abundance (July).

APPENDIX D

SUPPLEMENTARY MATERIAL FOR INFLUENCE OF RIVER DRYING AND INSECT AVAILABILITY ON BAT ACTIVITY ALONG THE SAN PEDRO RIVER, ARIZONA (USA)

TABLE 27. RM ANOVA results for bat activity, emergence rate, and aquatic, terrestrial, and total insect abundance and biomass related to class condition and month.

Source of Variation	*df*	SS	MS	*F*	*P*
Bat activity					
Condition class	1	0.243	0.243	0.337	0.580
Error (Condition class)	7	5.054	0.722		
Month	1	22.132	22.132	30.567	0.001
Error (Month)	7	5.068	0.724		
Condition class x Month	1	0.029	0.029	0.129	0.730
Error (Condition class x Month)	7	1.570	0.224		
Emergence rate					
Condition class	1	2.460	2.460	1.257	0.299
Error (Condition class)	7	13.704	1.958		
Month	1	1.354	1.354	1.141	0.321
Error (Month)	7	8.311	1.187		
Condition class x Month	1	1.405	1.405	0.972	0.357
Error (Condition class x Month)	7	10.118	1.445		
Aquatic insect abundance					
Condition class	1	0.076	0.076	0.124	0.739
Error (Condition class)	5	3.066	0.613		
Month	1	5.547	5.547	8.637	0.032
Error (Month)	5	3.211	0.642		
Condition class x Month	1	0.569	0.569	1.462	0.281
Error (Condition class x Month)	5	1.945	0.389		
Terrestrial insect abundance					
Condition class	1	1.101	1.101	0.685	0.445
Error (Condition class)	5	8.036	1.607		
Month	1	0.048	0.048	0.054	0.826
Error (Month)	5	4.472	0.894		
Condition class x Month	1	1.393	1.393	2.291	0.191
Error (Condition class x Month)	5	3.041	0.608		

Total insect abundance					
Condition class	1	0.990	0.990	0.507	0.508
Error (Condition class)	5	9.760	1.952		
Month	1	2.282	2.282	6.043	0.057
Error (Month)	5	1.888	0.378		
Condition class x Month	1	0.009	0.009	0.042	0.846
Error (Condition class x Month)	5	1.028	0.206		
Aquatic insect biomass					
Condition class	1	0.008	0.008	0.018	0.898
Error (Condition class)	5	2.210	0.442		
Month	1	4.274	4.274	4.912	0.077
Error (Month)	5	4.351	0.870		
Condition class x Month	1	0.160	0.160	0.299	0.608
Error (Condition class x Month)	5	2.672	0.534		
Terrestrial insect biomass					
Condition class	1	1.020	1.020	0.671	0.450
Error (Condition class)	5	7.595	1.519		
Month	1	0.130	0.130	0.187	0.684
Error (Month)	5	3.495	0.699		
Condition class x Month	1	0.777	0.777	1.202	0.323
Error (Condition class x Month)	5	3.231	0.646		
Total insect biomass					
Condition class	1	1.309	1.309	0.839	0.402
Error (Condition class)	5	7.803	1.561		
Month	1	0.147	0.147	0.357	0.576
Error (Month)	5	2.052	0.410		
Condition class x Month	1	0.234	0.234	0.639	0.460
Error (Condition class x Month)	5	1.833	0.367		

Notes: Data were ln transformed to meet assumptions of RM ANOVA.

TABLE 28. RM ANOVA results for bat activity by 4 ecomorphological functional groups related to class condition and month.

Source of Variation	df	SS	MS	*F*	*P*
High-FM bat activity					
Condition class	1	1.457	1.457	0.710	0.427
Error (Condition class)	7	14.376	2.054		
Month	1	31.685	31.685	32.215	0.001
Error (Month)	7	6.885	0.984		
Condition class x Month	1	2.054	2.054	1.890	0.212
Error (Condition class x Month)	7	7.608	1.087		
Low-FM bat activity					
Condition class	1	0.369	0.369	0.184	0.681
Error (Condition class)	7	14.004	2.001		
Month	1	10.429	10.429	20.060	0.003
Error (Month)	7	3.639	0.520		
Condition class x Month	1	4.753	4.753	7.635	0.028
Error (Condition class x Month)	7	4.357	0.622		
High-CF bat activity					
Condition class	1	0.001	0.001	0.341	0.578
Error (Condition class)	7	0.020	0.003		
Month	1	9.107E-5	9.107E-5	0.037	0.853
Error (Month)	7	0.017	0.002		
Condition class x Month	1	0.001	0.001	0.544	0.485
Error (Condition class x Month)	7	0.013	0.002		
Low-CF bat activity					
Condition class	1	0.928	0.928	4.825	0.064
Error (Condition class)	7	1.346	0.192		
Month	1	3.610	3.610	6.959	0.034
Error (Month)	7	3.631	0.519		
Condition class x Month	1	0.353	0.353	1.830	0.218
Error (Condition class x Month)	7	1.351	0.193		

Notes: Data were ln transformed to meet assumptions of RM ANOVA.

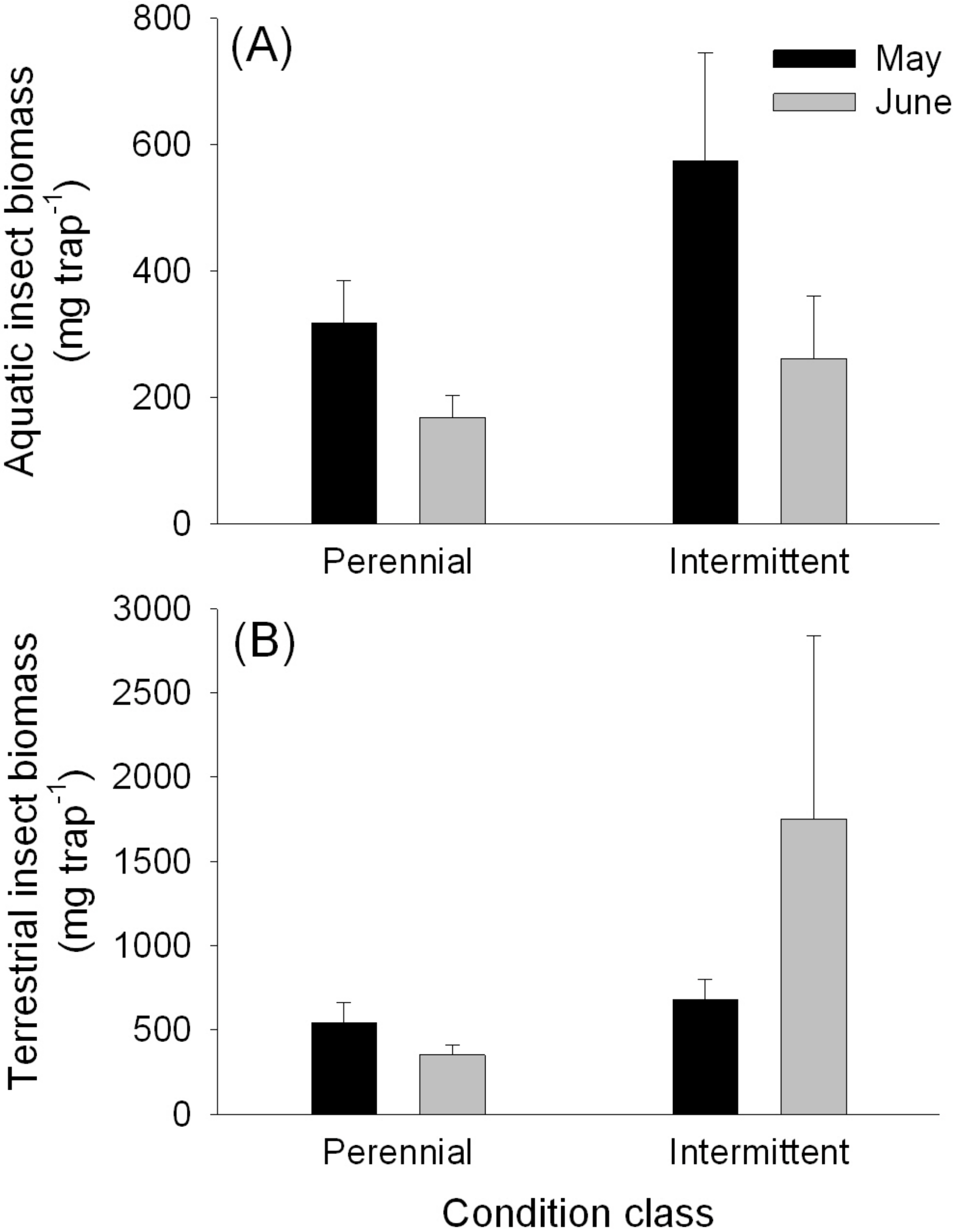


FIG. 38. Mean (± SE) aquatic (A) and terrestrial (B) insect biomass at sites in perennial and intermittent condition classes.

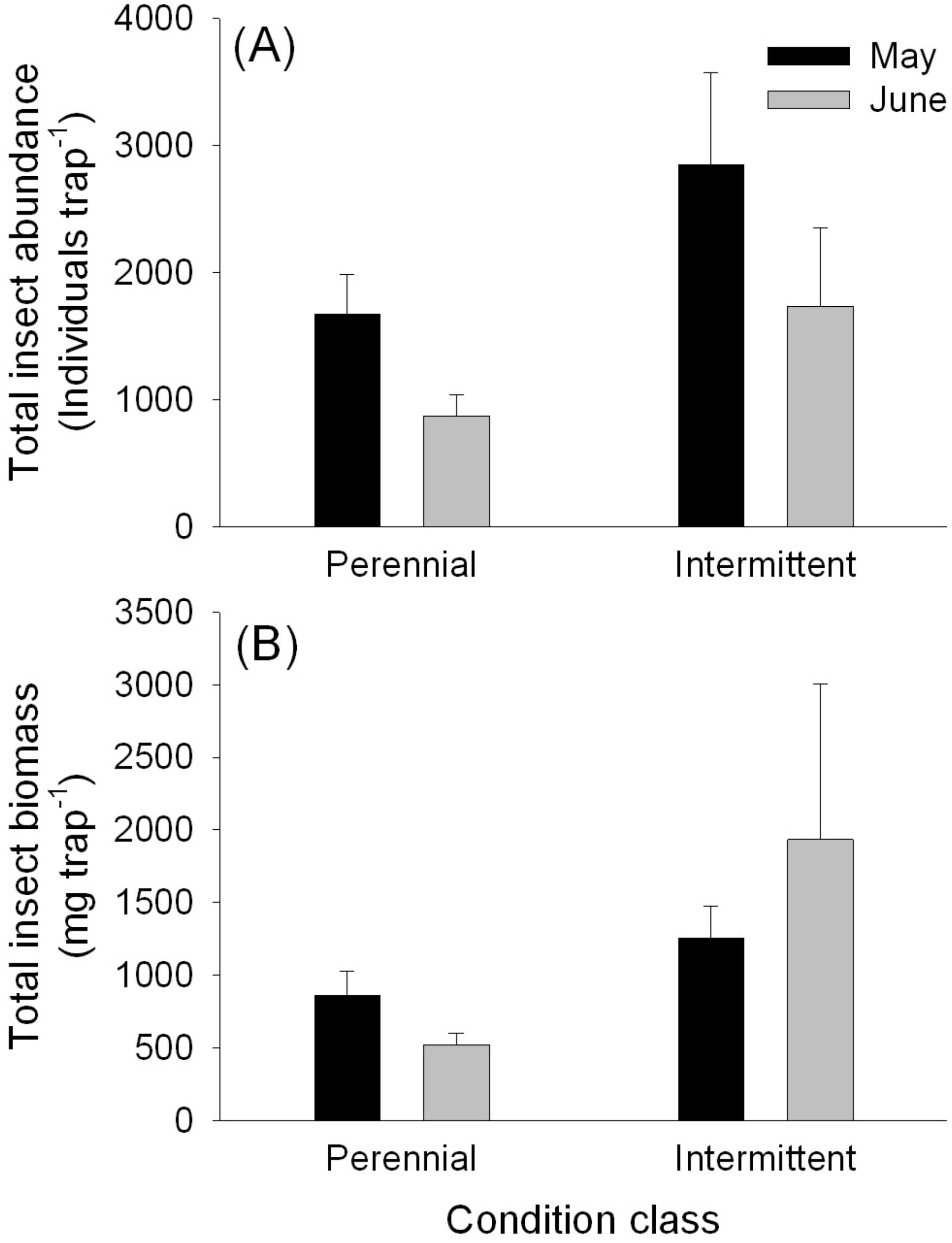


FIG. 39. Mean (± SE) total insect abundance (A) and biomass (B) at sites in perennial and intermittent condition classes.

TABLE 29. Bat species captured along the San Pedro River.

Date	Site	*Myotis velifer*	*Myotis californicus*	*Myotis occultus*	*Lasiurus blossevillii*	*Tadarida brasiliensis*	*Eptesicus fuscus*	*Lasiurus cinereus*	*Nyctinomops macrotis*	*Lasiurus xanthinus*	Unidentified	Total
12 May 2007	Grayhawk	2	0	0	0	2	0	1	0	0	3	8
18 May 2007	Lewis Springs	1	0	0	1	0	2	2	0	0	0	6
19 May 2007	Charleston	0	0	0	0	8	2	1	0	0	0	11
1 Jun 2007	Grayhawk	5	0	0	1	11	4	0	0	0	0	21
2 Jun 2007	Hereford - North	2	0	0	0	2	0	0	0	0	0	4
15 Jun 2007	Charleston	4	0	0	0	9	0	0	0	0	0	13
16 Jun 2007	Lewis Springs	2	0	0	1	6	4	0	0	0	0	13
29 Jun 2007	Grayhawk	0	0	0	1	1	1	0	0	0	0	3
30 Jun 2007	Hereford - South	0	1	1	1	5	8	0	1	0	0	17
14 Jul 2007	Charleston	0	0	0	0	0	0	0	0	1	0	1
17 Aug 2007	Charleston	0	0	0	0	0	0	0	0	0	0	0
8 Sep 2007	Charleston	2	0	0	0	0	0	0	0	0	0	2
	Total	18	1	1	5	44	21	4	1	1	3	99

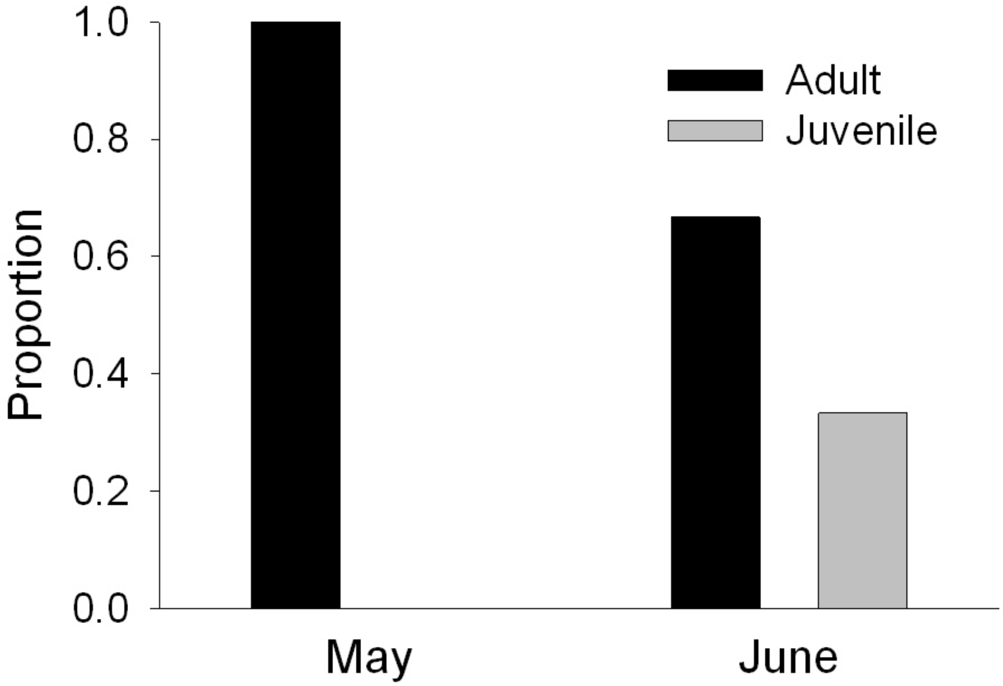


FIG. 40. Proportion of adult and juvenile bats captured along the San Pedro River in May and June 2007.

APPENDIX E

SUPPLEMENTARY MATERIAL FOR TEMPORAL VARIABILITY IN TERRESTRIAL CONSUMER DISTRIBUTIONS ALONG TWO DESERT STREAMS WITH CONTRASTNG PATTERNS OF PREY RESOURCE SUPPLY

TABLE 30. Measured values of biological and physical parameters in Sycamore Creek and San Pedro River during the study period.

Parameter	Sycamore Creek					San Pedro River				
	Mean	SE	Min	Max	N	Mean	SE	Min	Max	N
Aquatic aerial insect abundance above stream (ind./trap)[b]	611.8	313.1	5.2	3825.7	12	387.1	123.3	81.0	1144.3	11
Aquatic aerial insect abundance in floodplain (ind./trap)	148.4	80.1	3.1	1006.7	12	46.0	14.8	5.2	175.6	12
Terrestrial aerial insect abundance above stream (ind./trap)[b]	50.6	14.1	0.0	118.4	12	134.9	39.9	0.0	397.9	11
Terrestrial aerial insect abundance in floodplain (ind./trap)	43.2	14.4	0.0	161.5	12	44.6	13.2	5.2	164.1	12
Total aerial insects abundance above stream (ind./trap)[b]	662.4	315.4	5.2	3876.6	12	522.0	126.0	88.3	1269.5	11
Total aerial insects abundance in floodplain (ind./trap)	191.6	83.7	3.1	1064.9	12	90.6	24.2	10.4	283.6	12
Aquatic insect emergence (ind. m^{-2} day^{-1})	99.8	39.8	0.4	421.9	12	22.9	7.5	0.0	82.9	12
Benthic insect abundance (ind./trap)	38.6	17.2	1.3	200.2	12	15.5	5.1	0.0	51.2	12

Notes: SE is standard error; min is minimum; max is maximum; N is number of months sampled.

TABLE 31. RM ANOVA results for chlorophyll *a* concentration and periphyton biomass at each study site.

Source of variation	df	SS	MS	F	P
Sycamore Creek					
Chlorophyll a concentration					
Between Subjects	2	82473.290	41236.645		
Between Treatments	2	287592.178	143796.089	3.892	0.115
Residual	4	147797.668	36949.417		
Total	8	517863.136			
Periphyton biomass					
Between Subjects	2	78.199	39.099		
Between Treatments	2	116.196	58.098	6.627	0.054
Residual	4	35.066	8.766		
Total	8	229.460			
San Pedro River					
Chlorophyll a concentration					
Between Subjects	2	2957.547	1478.773		
Between Treatments	2	13908.323	6954.162	8.613	0.036
Residual	4	3229.566	807.391		
Total	8	20095.436			
Periphyton biomass					
Between Subjects	2	57.294	28.647		
Between Treatments	2	185.233	92.617	12.289	0.020
Residual	4	30.147	7.537		
Total	8	272.674			

Notes: Data are from pre-monsoon (May), post-monsoon (September), and winter (January) sampling periods.

TABLE 32. Mean (± SE) emergent aquatic insect length (mm) of Chironomidae, Chaoboridae, and Baetidae collected monthly in Sycamore Creek and the San Pedro River.

	Chironomidae		Chaoboridae		Baetidae	
Month	Sycamore Creek	San Pedro River	Sycamore Creek	San Pedro River	Sycamore Creek	San Pedro River
February	-	1.0 (0.0)	3.0 (0.0)	-	-	-
March	3.1 (0.2)	2.5 (0.0)	3.5 (0.0)	2.3 (0.3)	-	4.6 (0.4)
April	2.1 (0.2)	1.7 (0.2)	2.2 (0.1)	2.7 (0.2)	6.0 (0.0)	4.2 (0.8)
May	4.0 (0.2)	2.3 (0.2)	3.1 (0.1)	2.0 (0.0)	7.2 (1.0)	3.7 (0.0)
June	3.3 (0.4)	1.3 (0.0)	2.2 (0.4)	1.0 (0.0)	6.8 (2.3)	3.0 (0.0)
July	2.4 (0.6)	1.0 (0.0)	2.9 (0.4)	1.5 (0.0)	5.3 (0.1)	5.1 (0.0)
August	2.6 (0.3)	-	-	-	3.7 (0.4)	-
September	2.8 (0.1)	1.5 (0.0)	2.2 (0.3)	-	6.3 (0.0)	3.0 (0.0)
October	2.7 (0.1)	1.9 (0.1)	2.2 (0.2)	2.6 (0.0)	4.5 (0.0)	3.3 (0.2)
November	2.5 (1.0)	2.8 (0.4)	-	2.3 (0.4)	-	4.5 (0.3)
December	1.4 (0.2)	2.7 (0.3)	2.5 (0.0)	2.9 (0.1)	-	5.2 (0.3)
January	-	3.0 (0.4)	-	3.1 (0.2)	-	5.0 (0.3)
Annual average	2.7 (0.2)	2.0 (0.2)	2.6 (0.2)	2.3 (0.2)	5.7 (0.5)	4.2 (0.3)

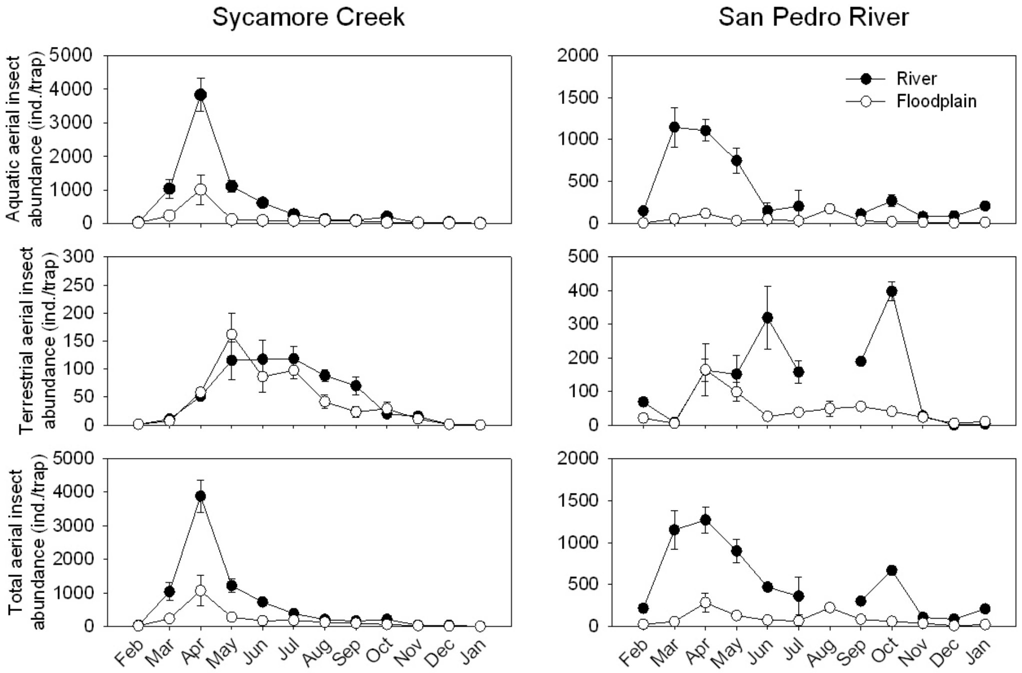


FIG. 41. Temporal variation of aquatic, terrestrial and total aerial insect abundance at Sycamore Creek and San Pedro River. Data are mean (± SE) values from monthly sampling conducted February 2008 – January 2009. Filled circles denote samples collected above the stream and open circles denote samples collected 25-m from the stream in the floodplain. Note different scales for Sycamore Creek and the San Pedro River.

TABLE 33. Numbers of bats captured at Sycamore Creek.

Month	*Myotis californicus*		*Myotis velifer*		*Myotis yumanensis*		*Lasionycteris noctivagans*		*Eptesicus fuscus*		*Lasiurus cinereus*		*Antrozous pallidus*		*Corynorhinus townsendii pallescens*		Total
	S	F	S	F	S	F	S	F	S	F	S	F	S	F	S	F	
February	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
April	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
May	0	0	1	0	0	0	1	0	3	0	1	0	0	0	0	0	6
June	0	0	2	0	6	0	0	0	1	0	0	0	1	0	0	0	10
July	1	0	10	0	2	0	0	0	1	0	0	0	0	0	0	0	14
August																	
September																	
October	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	3
November	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
December																	
January																	
Total bats captured	2	0	13	0	8	0	3	0	5	0	1	0	2	0	1	0	35

Notes: Bats were captured during 4-hr capture nights at each stream during study period (February 2008 – January 2009). We were unable to mist net in August and September due to rain. We were unable to capture bats in December and January because nighttime temperatures were below 10°C. S is stream; F is floodplain.

TABLE 34. Numbers of bats captured at San Pedro River.

Month	*Macrotus californicus*		*Myotis auriculus*		*Myotis velifer*		*Myotis yumanensis*		*Eptesicus fuscus*		*Lasiurus cinereus*		*Antrozous pallidus*		*Tadarida brasiliensis*		Total
	S	F	S	F	S	F	S	F	S	F	S	F	S	F	S	F	
February	0	1	0	0	0	0	3	0	0	0	0	0	0	0	1	0	5
March	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
April	0	0	0	0	3	0	2	0	0	0	3	0	3	0	0	0	11
May	1	1	1	0	1	0	0	0	2	0	0	0	3	0	0	0	9
June[a]																	
July	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	3
August[a]																	
September	0	0	0	0	4	0	0	0	0	0	0	0	1	3	0	0	8
October	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
November	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
December[b]																	
January[b]																	
Total bats captured	2	3	1	0	8	0	8	0	2	0	3	0	7	5	1	0	40

Notes: Bats were captured during 4-hr capture nights at each stream during study period (February 2008 – January 2009). We were unable to mist net in June and August due to rain. We were unable to capture bats in December and January because nighttime temperatures were below 10°C. S is stream; F is floodplain.

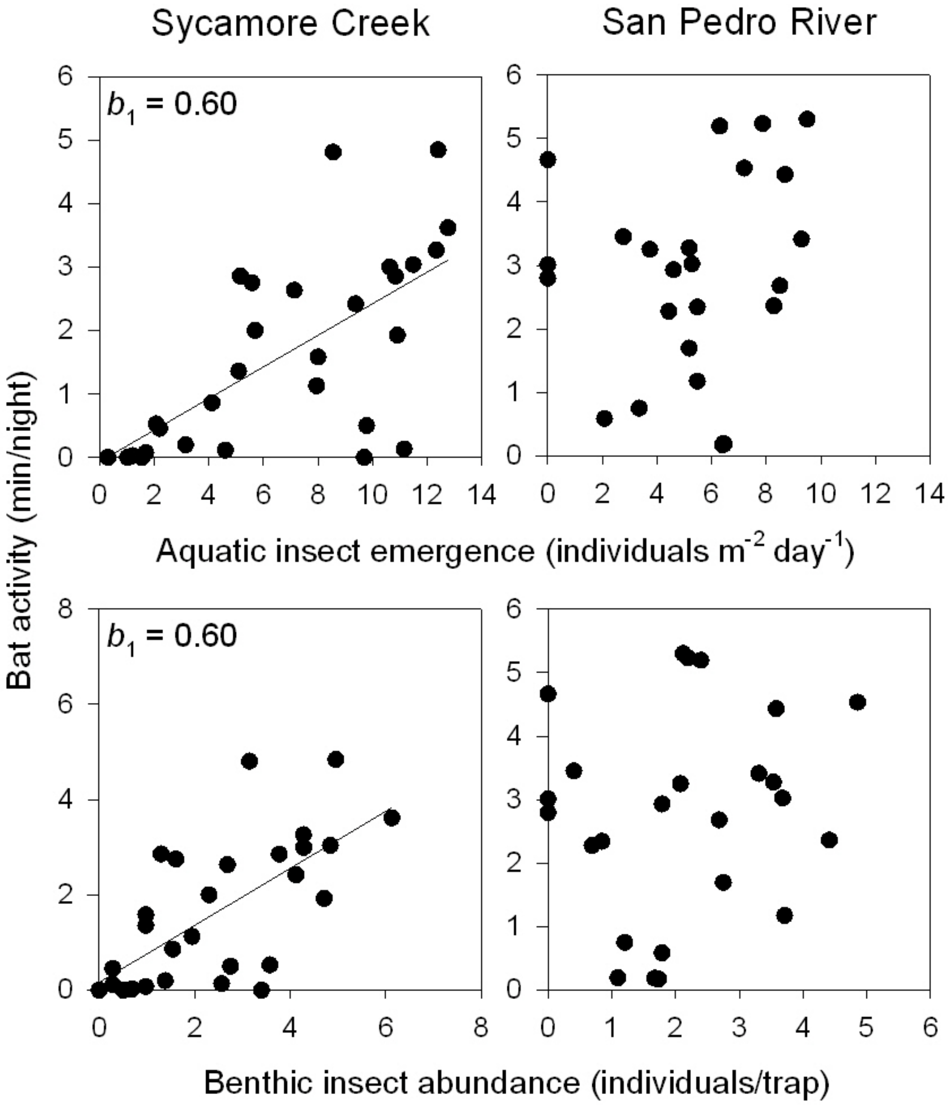


FIG. 42. Relationship between bat acoustic activity and aquatic insect emergence and benthic insect abundance at Sycamore Creek and the San Pedro River. Data are monthly values from each study site. Filled circles denote samples collected above the stream and open circles denote samples collected 25-m from the stream in the floodplain. Data were ln +1 transformed. b_1 = slope.

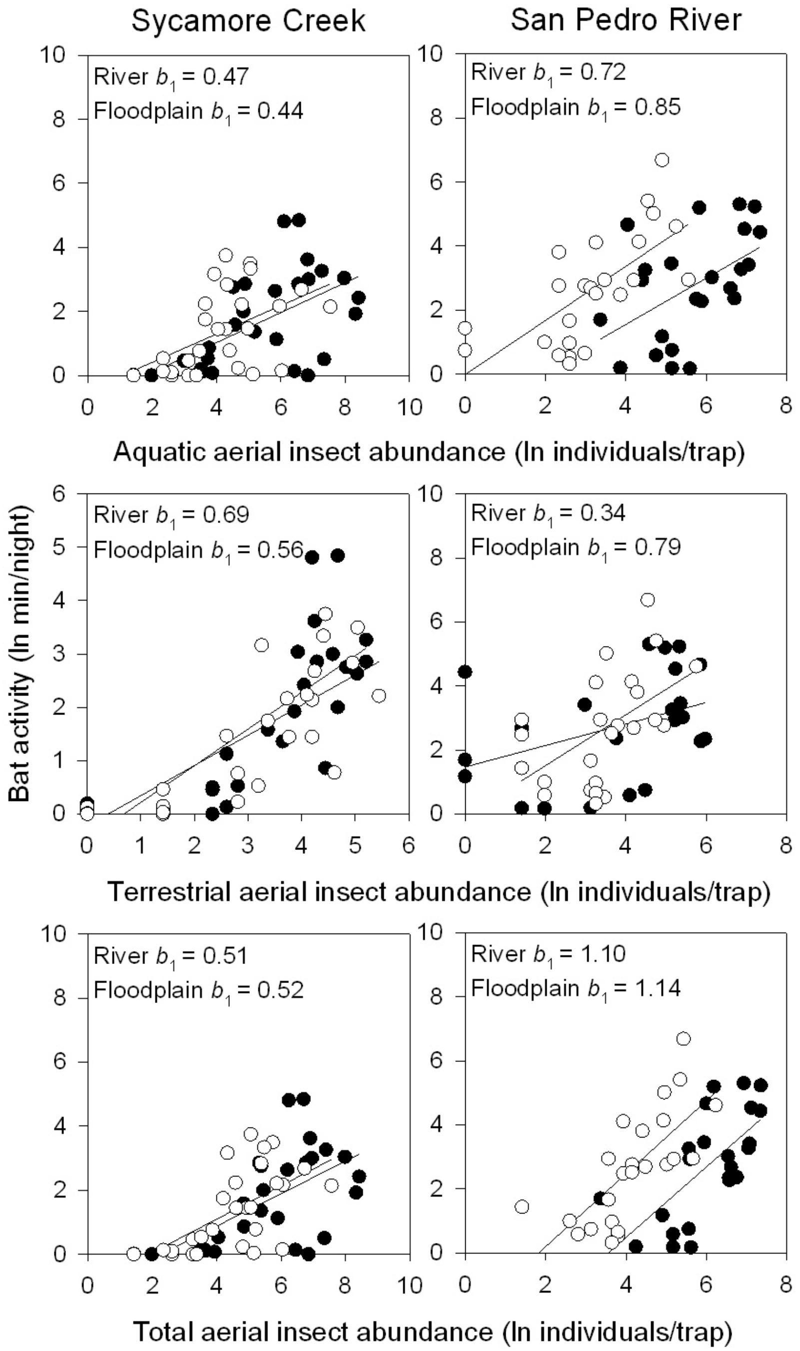


FIG. 43. Relationship between bat acoustic activity and aquatic and terrestrial aerial insect abundance at Sycamore Creek and the San Pedro River. Data are monthly values from each study site. Filled circles denote samples collected above the stream and open circles denote samples collected 25-m from the stream in the floodplain. Data were ln +1 transformed. b_1 = slope.

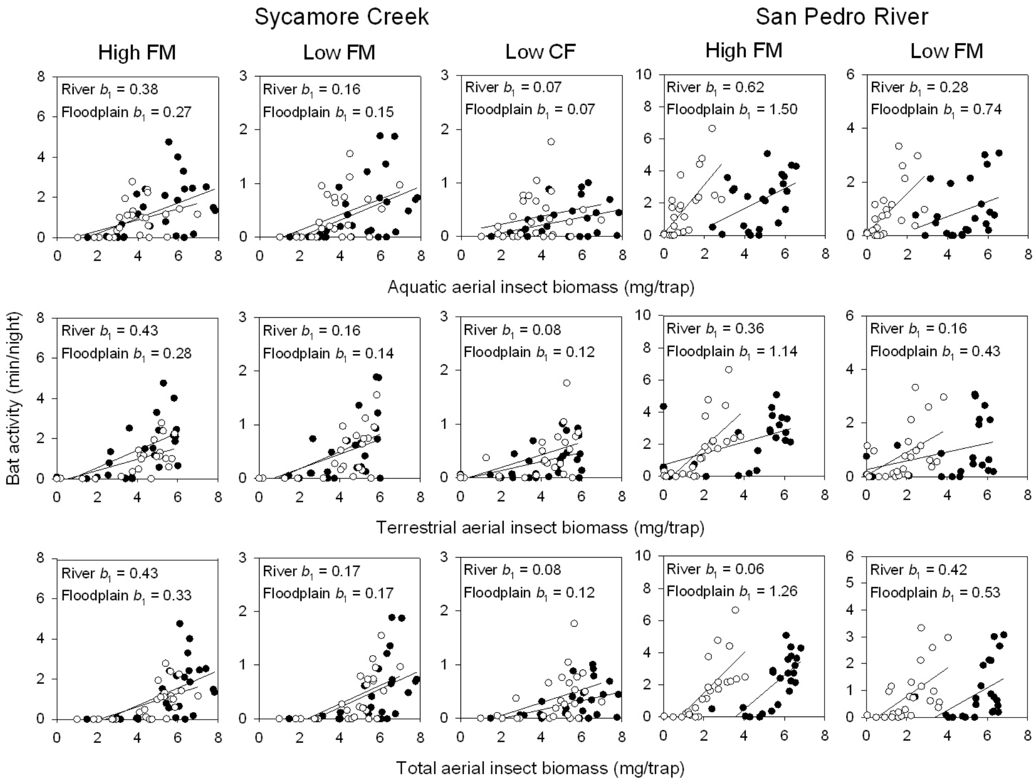


FIG. 44. Relationship between high-frequency modulated (high-FM), low-frequency modulated (low-FM), and low-constant frequency (low-CF) bats and aquatic and terrestrial aerial insect biomass at Sycamore Creek and the San Pedro River. Data are paired monthly values from each study site. Filled circles denote samples collected above the stream and open circles denote samples collected 25-m from the stream in the floodplain. Data were ln +1 transformed. b_1 = slope.

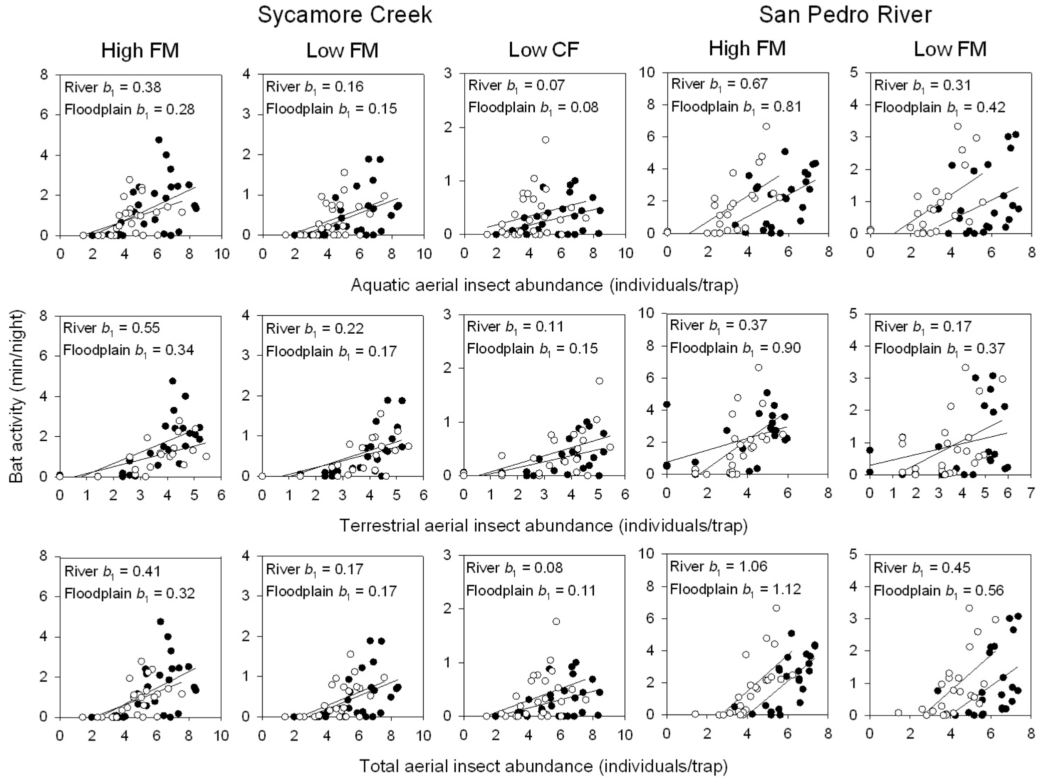


FIG. 45. Relationship between high-frequency modulated (high-FM), low-frequency modulated (low-FM), and low-constant frequency (low-CF) bats and aquatic, terrestrial, and total aerial insect abundance at Sycamore Creek and the San Pedro River. Data are monthly values from each study site. Filled circles denote samples collected above the stream and open circles denote samples collected 25-m from the stream in the floodplain. Data were ln +1 transformed. b_1 = slope.

TABLE 35. Pearson product-moment correlations between bat activity and insect standing stocks, water temperature, and air temperature.

	Sycamore Creek		San Pedro River	
Total bats	Stream	Floodplain	Stream	Floodplain
Aquatic aerial insect abundance (ind./trap)	0.59, 0	0.52, 0.01	0.5, 0.01	0.68, 0
Terrestrial aerial insect abundance (ind./trap)	0.8, 0	0.81, 0	-	0.53, 0.01
Total aerial insects abundance (ind./trap)	0.62, 0	0.63, 0	0.67, 0	0.71, 0
Aquatic insect emergence (ind. m^{-2} day^{-1})	0.66, 0	0.52, 0	-	-
Benthic insect abundance (ind./trap)	0.68, 0	0.51, 0.01	-	-
Water temperature (°C)	0.7, 0	0.72, 0	0.65, 0	0.78, 0
Air temperature (°C)	0.75, 0	0.76, 0	0.57, 0.01	0.77, 0
High-frequency modulated bats				
Aquatic aerial insect biomass (mg/trap)	0.53, < 0.01	0.48, 0.01	0.47, 0.02	0.68, < 0.01
Terrestrial aerial insect biomass (mg/trap)	0.67, < 0.01	0.74, < 0.01	0.5, 0.02	0.71, < 0.01
Total aerial insect biomass (mg/trap)	0.59, < 0.01	0.66, < 0.01	0.73, < 0.01	0.75, < 0.01
Aquatic aerial insect abundance (ind./trap)	0.53, 0	0.49, 0.01	0.5, 0.02	0.64, 0
Terrestrial aerial insect abundance (ind./trap)	0.73, 0	0.75, 0	0.47, 0.02	0.59, 0
Total aerial insects abundance (ind./trap)	0.56, 0	0.58, 0	0.68, 0	0.69, 0
Aquatic insect emergence (ind. m^{-2} day^{-1})	0.63, 0	0.45, 0.02	-	-
Aquatic insect emergence (mg m^{-2} day^{-1})	0.67, 0	0.5, 0.01	-	-
Benthic insect abundance (ind./trap)	0.64, 0	0.44, 0.02	-	-
Benthic insect biomass (mg/trap)	0.52, 0	-	-	-
Water temperature (°C)	0.67, 0	0.71, 0	0.69, 0	0.8, 0
Air temperature (°C)	0.72, 0	0.73, 0	0.62, 0	0.8, 0

Low-frequency modulated bats				
Aquatic aerial insect biomass (mg/trap)	0.52, 0	0.47, 0.01	0.33, 0.13	0.6, 0
Terrestrial aerial insect biomass (mg/trap)	0.6, 0	0.66, 0	0.36, 0.1	0.48, 0.02
Total aerial insect biomass (mg/trap)	0.56, 0	0.63, 0	0.45, 0.03	0.56, 0
Aquatic aerial insect abundance (ind./trap)	0.52, 0	0.49, 0.01	0.35, 0.1	0.6, 0
Terrestrial aerial insect abundance (ind./trap)	0.68, 0	0.68, 0	0.33, 0.12	0.44, 0.03
Total aerial insects abundance (ind./trap)	0.55, 0	0.57, 0	0.45, 0.03	0.62, 0
Aquatic insect emergence (ind. m^{-2} day^{-1})	0.63, 0	0.49, 0.01	-	-
Aquatic insect emergence (mg m^{-2} day^{-1})	0.66, 0	0.57, 0	-	-
Benthic insect abundance (ind./trap)	0.67, 0	0.56, 0	-	-
Benthic insect biomass (mg/trap)	0.62, 0	-	-	-
Water temperature (°C)	0.55, 0	0.51, 0.02	-	0.54, 0.03
Air temperature (°C)	0.54, 0	0.61, 0	-	0.52, 0.01
Low-constant frequency bats				
Aquatic aerial insect biomass (mg/trap)	0.43, 0.02	-	-	-
Terrestrial aerial insect biomass (mg/trap)	0.55, < 0.01	0.59, < 0.01	-	-
Total aerial insect biomass (mg/trap)	0.48, 0.01	0.47, 0.01	-	-
Aquatic aerial insect abundance (ind./trap)	0.43, 0.02	-	-	-
Terrestrial aerial insect abundance (ind./trap)	0.62, 0	0.63, 0	-	-
Total aerial insects abundance (ind./trap)	0.45, 0.01	0.39, 0.04	-	-
Aquatic insect emergence (ind. m^{-2} day^{-1})	0.48, 0.01	0.43, 0.03	-	-
Aquatic insect emergence (mg m^{-2} day^{-1})	0.4, 0.03	0.46, 0.02	-	-
Benthic insect abundance (ind./trap)	0.53, 0	-	-	-
Benthic insect biomass (mg/trap)	0.46, 0.01	0.26, 0.2	-	-
Water temperature (°C)	0.5, 0.01	0.5, 0.02	-	0.53, 0.03
Air temperature (°C)	0.55, 0	0.54, 0.01	-	-

Bat capture rate				
Aquatic aerial insect abundance (ind./trap)	-	-	-	-
Terrestrial aerial insect abundance (ind./trap)	-	-	-	-
Total aerial insects abundance above the river (ind./trap)	-	-	-	-
Total aerial insects abundance in floodplain (ind./trap)	-	-	0.76, 0.03	-
Aquatic insect emergence (ind. m^{-2} day^{-1})	-	-	-	-
Benthic insect abundance (ind./trap)	0.76, 0.03	-	-	-
Water temperature (°C)	0.81, 0.01	-	-	-
Air temperature above stream (°C)	0.78, 0.04	-	-	-
Air temperature in floodplain (°C)	0, 0	-	-	-

Notes: Data are monthly values from each site at Sycamore Creek and the San Pedro River. Pearson correlation coefficient and *P* values are shown for significant relationships. Data were ln +1 transformed. Dashes (-) indicate non-significant relationships.

TABLE 36. Percentage emergent, aerial, and benthic insect orders collected monthly from Sycamore Creek.

	F	M	A	M	J	J	A	S	O	N	D	J
Emergent aquatic insects												
Ephemeroptera	0.3	0.0	0.0	0.8	0.5	9.8	15.7	5.6	2.2	3.3	11.1	0.0
Odonata	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
Plecoptera	49.4	12.3	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemiptera	1.4	0.2	0.4	0.1	3.6	7.9	17.3	0.2	0.3	8.3	2.8	5.6
Coleoptera	0.0	0.2	1.0	0.4	0.1	16.8	4.1	0.0	0.5	12.0	0.0	0.0
Hymenoptera	0.0	0.0	0.3	0.1	0.1	2.7	0.0	0.4	0.2	2.2	0.0	0.0
Trichoptera	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diptera	48.9	87.4	97.3	98.7	94.7	62.0	62.9	93.8	96.8	74.2	86.1	94.4
Aquatic aerial insects above stream												
Ephemeroptera	0.0	0.0	0.0	3.2	0.3	0.6	5.2	1.1	8.0	13.1	0.0	0.0
Plecoptera	0.0	0.5	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Trichoptera	0.0	0.0	0.0	0.0	0.0	3.4	3.8	0.0	0.5	0.0	0.0	0.0
Diptera	100.0	99.5	100.0	96.8	99.7	95.6	91.0	98.9	91.4	86.9	100.0	100.0
Terrestrial aerial insects above stream												
Hemiptera	0.0	0.0	0.0	1.4	2.7	2.6	0.0	0.0	13.9	0.0	0.0	0.0
Homoptera	0.0	0.0	7.8	8.0	2.7	4.8	9.4	6.3	23.9	0.0	0.0	0.0
Thysanoptera	0.0	19.4	66.2	27.9	2.3	6.8	21.0	7.8	2.2	0.0	0.0	0.0
Psocoptera	0.0	16.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera	0.0	52.8	21.9	51.6	75.6	69.8	44.9	56.4	27.2	83.3	0.0	0.0
Hymenoptera	0.0	11.1	2.2	11.1	16.6	15.9	23.8	29.5	18.9	16.7	100.0	0.0
Lepidoptera	0.0	0.0	1.9	0.0	0.0	0.0	0.9	0.0	5.6	0.0	0.0	0.0
Diptera	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.3	0.0	0.0	0.0

Aquatic aerial insects in floodplain												
Hemiptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	11.1	0.0	0.0	0.0
Neuroptera	0.0	0.0	0.0	1.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichoptera	0.0	0.0	0.0	1.4	0.0	2.4	0.5	0.0	0.0	0.0	0.0	0.0
Diptera	100.0	100.0	100.0	97.6	98.9	97.6	99.5	97.2	88.9	100.0	100.0	100.0
Terrestrial aerial insects in floodplain												
Hemiptera	0.0	0.0	0.0	2.2	2.6	3.0	0.0	5.6	3.7	33.3	0.0	0.0
Homoptera	0.0	0.0	11.9	12.2	13.1	7.7	14.4	16.7	29.8	16.7	100.0	0.0
Thysanoptera	0.0	0.0	62.5	64.2	18.1	30.5	10.5	30.6	28.3	0.0	0.0	0.0
Psocoptera	0.0	44.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera	100.0	55.6	17.1	5.2	26.2	21.5	30.5	16.7	22.8	25.0	0.0	0.0
Hymenoptera	0.0	0.0	8.4	16.2	40.0	37.3	44.6	30.6	15.4	25.0	0.0	0.0
Benthic aquatic insects												
Ephemeroptera	25.0	0.0	4.4	18.9	0.3	0.0	43.7	4.2	19.2	10.0	15.0	5.6
Odonata	0.0	0.0	0.0	0.0	16.7	4.2	2.0	2.1	8.1	15.9	17.8	0.0
Plecoptera	66.7	30.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemiptera	0.0	0.0	0.0	0.0	3.5	0.0	3.3	3.7	7.4	1.0	2.8	0.0
Coleoptera	0.0	5.9	18.8	19.0	10.0	17.2	9.7	59.5	23.6	9.5	8.3	71.1
Trichoptera	0.0	0.0	0.0	0.0	0.2	0.0	4.6	0.0	4.4	39.1	46.4	2.2
Diptera	8.3	64.1	76.8	59.9	69.3	78.6	36.7	30.6	37.3	24.6	9.7	21.1

TABLE 37. Percentage emergent, aerial, and benthic insect orders collected monthly from the San Pedro River.

	F	M	A	M	J	J	A	S	O	N	D	J
Emergent aquatic insects												
Ephemeroptera	10.6	0.4	5.3	12.3	3.3	14.4	-	14.1	6.7	1.8	6.4	6.0
Odonata	0.0	0.0	0.0	0.0	3.6	0.0	-	0.0	1.4	0.0	0.0	0.0
Plecoptera	0.0	1.4	0.0	0.0	0.0	0.0	-	0.0	0.0	0.0	0.0	0.0
Hemiptera	27.8	0.2	2.7	22.0	0.0	14.4	-	0.0	1.9	0.7	1.1	1.8
Coleoptera	10.4	0.1	7.0	12.8	26.6	46.3	-	46.3	17.6	8.1	0.4	1.7
Hymenoptera	0.0	0.0	0.2	0.3	1.9	0.0	-	0.0	2.6	0.3	0.0	0.2
Trichoptera	0.0	0.0	0.2	8.4	2.4	1.1	-	0.0	0.0	0.0	0.0	0.0
Lepidoptera	0.0	0.0	0.0	0.2	0.0	0.0	-	0.0	0.0	0.0	0.0	0.0
Diptera	51.2	97.9	84.6	44.2	62.2	23.7	-	39.6	69.8	89.1	92.1	90.3
Aerial aquatic insects above stream												
Ephemeroptera	26.3	3.4	10.2	13.7	9.7	20.1	-	0.9	9.0	3.6	5.8	6.6
Trichoptera	0.0	0.1	0.1	0.4	0.4	0.0	-	0.0	0.5	0.0	0.0	0.9
Diptera	73.7	96.6	89.7	85.9	89.9	79.9	-	99.1	90.5	96.4	94.2	92.5
Aerial terrestrial insects above stream												
Hemiptera	0.0	0.0	0.0	1.3	1.1	0.5	-	2.3	0.9	0.0	-	0.0
Homoptera	0.0	0.0	6.7	1.3	0.4	0.0	-	3.1	0.6	5.0	-	0.0
Thysanoptera	0.0	16.7	12.8	4.8	0.4	2.0	-	2.9	3.1	13.0	-	50.0
Coleoptera	100.0	66.7	69.2	77.8	90.1	85.7	-	85.2	92.4	70.9	-	50.0
Hymenoptera	0.0	16.7	10.6	10.0	8.0	11.8	-	2.8	1.9	11.1	-	0.0
Lepidoptera	0.0	0.0	0.7	0.6	0.0	0.0	-	0.0	0.8	0.0	-	0.0
Diptera	0.0	0.0	0.0	4.2	0.0	0.0	-	3.7	0.4	0.0	-	0.0

Aerial aquatic insects in floodplain												
Ephemeroptera	0.0	0.0	0.0	16.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aquatic Hemiptera	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0
Trichoptera	0.0	0.0	1.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diptera	100.0	100.0	99.0	77.8	100.0	100.0	98.5	100.0	100.0	100.0	100.0	100.0
Aerial terrestrial insects in floodplain												
Hemiptera	0.0	0.0	0.0	4.8	0.0	4.4	7.5	6.3	14.8	7.4	0.0	0.0
Homoptera	5.6	0.0	10.1	17.7	33.3	9.2	4.2	4.4	7.5	6.0	16.7	77.8
Thysanoptera	11.1	41.7	45.1	23.4	6.5	9.2	11.4	27.8	9.4	40.7	33.3	18.1
Coleoptera	83.3	33.3	32.3	32.6	17.6	25.6	50.5	35.9	41.3	18.1	16.7	4.2
Hymenoptera	0.0	25.0	11.0	13.1	42.6	51.6	22.3	9.3	8.2	16.7	33.3	0.0
Diptera	0.0	0.0	1.6	8.4	0.0	0.0	4.2	16.3	18.7	11.1	0.0	0.0
Benthic insects												
Ephemeroptera	4.4	13.2	5.2	39.3	30.0	0.0	-	0.0	0.0	11.1	11.0	22.7
Odonata	12.7	1.0	2.8	6.7	17.0	4.6	-	0.0	16.7	5.6	5.1	0.6
Hemiptera	0.7	0.0	0.0	8.5	33.7	23.0	-	2.2	0.0	0.0	0.3	6.4
Coleoptera	38.5	6.6	33.8	24.5	17.5	43.1	-	97.8	83.3	72.2	23.0	35.0
Megaloptera	0.0	0.0	0.1	0.0	0.0	0.0	-	0.0	0.0	0.0	1.4	0.3
Trichoptera	0.0	0.0	0.0	8.5	0.0	0.0	-	0.0	0.0	0.0	1.1	9.8
Diptera	43.7	79.2	58.1	12.5	1.8	29.3	-	0.0	0.0	11.1	58.1	25.3

Notes: August emergent, aerial, and benthic insect samples were lost due to a monsoon flood. Zero terrestrial aerial insects were collected on sticky traps in December.

APPENDIX F

SUPPLEMENTARY MATERIAL FOR EFFECTS OF AQUATIC INSECT AVAILABLITY AND RIPARIAN VEGETATION STRUCTURE ON BAT ACTIVITY

TABLE 38. Results from 2-way ANOVA using fixed effects models with 2 main effects (reach and treatment) but no interaction terms.

Source of Variation	*df*	SS	MS	*F*	*P*
Aquatic insect abundance					
Treatment	1	0.783	0.783	8.420	0.211
Reach	1	0.497	0.497	5.343	0.260
Residual	1	0.0930	0.0930		
Total	3	1.373	0.458		
Terrestrial insect abundance					
Treatment	1	0.0702	0.0702	4.494	0.281
Reach	1	0.0462	0.0462	2.958	0.335
Residual	1	0.0156	0.0156		
Total	3	0.132	0.0440		
Bat acoustic activity					
Treatment	1	0.0169	0.0169	6.760	0.234
Reach	1	0.302	0.302	121.000	0.058
Residual	1	0.00250	0.00250		
Total	3	0.322	0.107		
Number of feeding buzzes					
Treatment	1	0.0702	0.0702	34.679	0.107
Reach	1	0.0156	0.0156	7.716	0.220
Residual	1	0.00202	0.00202		
Total	3	0.0879	0.0293		

Notes: Data were ln or ln + 1 transformed.

TABLE 39. Results from 3-way ANOVA using fixed effects models with 3 main effects (reach, treatment, and distance from river) but no interaction terms for aquatic insect abundance, terrestrial insect abundance, bat acoustic activity, and feeding buzzes.

Source of Variation	*df*	SS	MS	*F*	*P*
Aquatic insect abundance					
treatment	1	0.293	0.293	1.330	0.368
reach	1	0.673	0.673	3.058	0.222
distance	2	12.321	6.161	27.994	0.034
Residual	2	0.440	0.220		
Total	11	15.020	1.365		
Terrestrial insect abundance					
treatment	1	0.00723	0.00723	0.0415	0.857
reach	1	0.000974	0.000974	0.00559	0.947
distance	2	5.758	2.879	16.521	0.057
Residual	2	0.349	0.174		
Total	11	6.645	0.604		
Bat acoustic activity					
treatment	1	0.349	0.349	8.231	0.103
reach	1	0.356	0.356	8.394	0.101
distance	2	10.805	5.403	127.517	0.008
Residual	2	0.0847	0.0424		
Total	11	11.970	1.088		
Number of feeding buzzes					
treatment	1	0.215	0.215	0.576	0.527
reach	1	0.00824	0.00824	0.0221	0.895
distance	2	11.365	5.683	15.260	0.062
Residual	2	0.745	0.372		
Total	11	12.890	1.172		

Notes: Data were ln or ln + 1 transformed.

APPENDIX G

INSTITUTIONAL ANIMAL CARE & USE COMMITTEE ANIMAL PROTOCOLS

Institutional Animal Care and Use Committee (IACUC)
Arizona State University

Tempe, Arizona 85287-3503
(480) 965-2179 FAX: (480) 965-8013

Animal Protocol Review

Protocol Number:	06-848R
Protocol Title:	Effects of River channel Geomorphology and Riparian Vegetation Structure on Bat Foraging Ecology within the South Fork Eel Watershed, Mendocino County, California.
Principal Investigator:	John Sabo
Date of Action:	11/02/2005 Final Action Date: 11/02/2005

The animal protocol review was considered by the Committee and the following decisions were made:

☐ The original protocol was APPROVED as presented.
☒ The revised protocol was APPROVED as presented.
☐ The protocol was APPROVED with RESTRICTIONS or CHANGES as listed below. The project can only be pursued, subject to your acceptance of these restriction or changes. If you are not agreeable, contact the IACUC Chairperson immediately.
☐ The Committee requests CLARIFICATIONS or CHANGES in the protocol as described below. Approval is contingent upon review and approval of the required revisions by the IACUC Chair.
☐ The protocol was approved, subject to the approval of a WAIVER of provisions of NIH policy as noted below. Waivers require written approval from the granting agencies.
☐ The protocol was DISAPPROVED for reasons outlined in the attached memorandum.
☐ The Committee requests you to contact ________________ to discuss this proposal.
☐ A copy of this correspondence has been sent to the Vice President for Research.

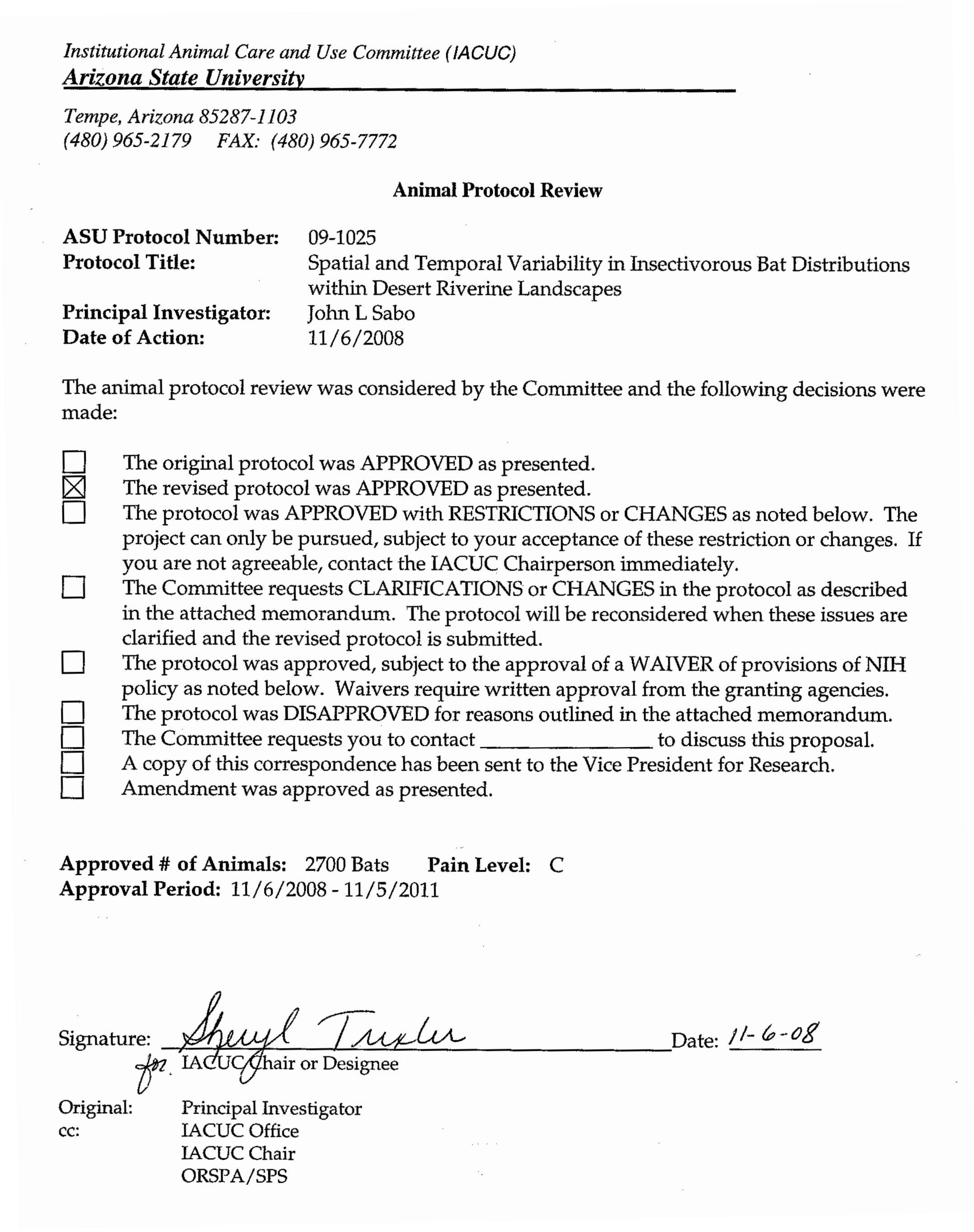
RESTRICTIONS, CHANGES OR WAIVER REQUIREMENT:

Approved number of Animals: 153 Bats

Approval Period: 11/02/2005 - 11/01/2008

Signature: ______________________________ Date: 11/02/2005
IACUC Chair ~~or Designee~~

Investigator cc: ~~IACUC~~ Office, IACUC Chair, ORSPA



Institutional Animal Care and Use Committee (IACUC)
Arizona State University

Tempe, Arizona 85287-1103
(480) 965-2179 FAX: (480) 965-7772

Animal Protocol Review

ASU Protocol Number: 09-1025
Protocol Title: Spatial and Temporal Variability in Insectivorous Bat Distributions within Desert Riverine Landscapes
Principal Investigator: John L Sabo
Date of Action: 11/6/2008

The animal protocol review was considered by the Committee and the following decisions were made:

☐ The original protocol was APPROVED as presented.
☒ The revised protocol was APPROVED as presented.
☐ The protocol was APPROVED with RESTRICTIONS or CHANGES as noted below. The project can only be pursued, subject to your acceptance of these restriction or changes. If you are not agreeable, contact the IACUC Chairperson immediately.
☐ The Committee requests CLARIFICATIONS or CHANGES in the protocol as described in the attached memorandum. The protocol will be reconsidered when these issues are clarified and the revised protocol is submitted.
☐ The protocol was approved, subject to the approval of a WAIVER of provisions of NIH policy as noted below. Waivers require written approval from the granting agencies.
☐ The protocol was DISAPPROVED for reasons outlined in the attached memorandum.
☐ The Committee requests you to contact ________________ to discuss this proposal.
☐ A copy of this correspondence has been sent to the Vice President for Research.
☐ Amendment was approved as presented.

Approved # of Animals: 2700 Bats **Pain Level:** C
Approval Period: 11/6/2008 - 11/5/2011

Signature: Sheryl Truxler ______________ Date: 11-6-08
for. IACUC Chair or Designee

Original: Principal Investigator
cc: IACUC Office
IACUC Chair
ORSPA/SPS