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Temporal variability in insectivorous bat activity along two desert streams with contrasting patterns of prey availability

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ABSTRACT

Emergent aquatic insects provide significant resources for terrestrial consumers. The availability and consumption of aquatic insects by terrestrial consumers may be influenced by characteristics of the river and riparian area. We measured temporal variability in bat activity and insect availability along two desert streams of contrasting productivity, hydrology, and riparian vegetation in Arizona, USA. Sycamore Creek is very productive, winter storm dominated, and supports sparse riparian vegetation. San Pedro River productivity is low, most floods occur during the summer monsoon, and it has extensive riparian vegetation. Bat activity and insect availability were measured monthly directly above the stream and in the floodplain for one year. At Sycamore Creek, emergent aquatic-insect biomass peaked in spring, while terrestrial-insect biomass was highest in the summer. Aquatic and terrestrial insect availability at the San Pedro River were similar or dominated by terrestrial insects throughout the spring and summer. Interactions between bats and insects differed between these two streams and this variation appears to be due to differences in insect availability in the airspace above the stream. Insect-prey availability is linked to stream productivity, timing of flooding, and the extent of riparian vegetation, and these factors can have strong effects on terrestrial food webs.

1. Introduction

The movement of energy, material, and organisms between rivers and the riparian zone closely links aquatic and terrestrial ecosystems. Much research has focused on the movement of aquatic insect between aquatic and terrestrial ecosystems and its effect on the abundance (Sabo and Power, 2002a), distribution (Iwata, 2007), and behavior (Nakano et al., 1999; Sabo and Power, 2002b) of terrestrial consumers. Emergent aquatic insects account for 25–100% of the energy supply to terrestrial predators (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 all of their energy requirements along a desert stream during a 6-week period in summer. While it is well established that aquatic insects provide a substantial portion of the diet of terrestrial consumers (e.g., Collier et al., 2002; Sanzone et al., 2003), most studies have been short of duration and have not considered temporal variability in the availability of emergent insects or its effects on terrestrial predators (but see Nakano and Murakami, 2001).

The emergence of aquatic insects is temporally variable (Corbet, 1964) and fluxes of aquatic resources from streams to land can vary considerably over time. Emergence from desert streams in the Southwestern United States is particularly variable and closely tied to the timing of floods (Lytle, 2002). In desert streams with a weak summer monsoon, aquatic insect emergence continues throughout the summer months (Jackson and Fisher, 1986) but where there is a strong summer monsoon, emergence occurs earlier, prior to the flood (Lytle, 2002). This pattern is significant because the strength of interactions between terrestrial consumers and aquatic resources may depend on the timing of aquatic insect emergence and may be weak where variability in aquatic resources is high. For example, bats successfully tracked the abundance of adult aquatic insects at perennial sites but not at intermittent sites where aquatic insect availability was more variable (Hagen and Sabo, 2012).

Previous studies showing strong effects of aquatic insects on terrestrial consumers have been generally conducted during peak aquatic insect emergence (e.g., Hagen and Sabo, 2011, 2012; Sabo and Power, 2002a, 2002b). Nakano and Murakami (2001) found that aquatic insects made up most of riparian bird diet (50–90%) from November to May in Japan after riparian trees had dropped their leaves and terrestrial insects were unavailable. However,

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when trees were in leaf and terrestrial insect biomass was high but aquatic insect biomass low, birds switched to terrestrial insects. Thus, temporal variability in aquatic insect availability may influence how well terrestrial consumers can track aquatic resources.

The structure, density, and composition of riparian vegetation may also affect the supply of aquatic insects to the land (Hagen and Sabo, 2011; Laeser et al., 2005). Desert river-riparian systems exhibit a wide range of forest physiognomies and hydrology, ranging from open ephemeral or intermittent channels bordered by occasional woody shrubs and little canopy cover to perennial rivers bordered by phreatophytic trees and full canopy closure by gallery forests. Reduced riparian habitat, high stream primary productivity, high water temperature, intermittent flow, and flash floods characterize many desert streams, especially those with sparse trees. These conditions contribute to high rates of secondary production (Fisher and Gray, 1983; Jackson and Fisher, 1986), and abundant supply of insects (Jackson and Fisher, 1986), short invertebrate life cycles (Gray, 1981), and rapid recovery after 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, and relatively low stream 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 hydrological extremes. Floods and droughts may or may not coincide with the peak growing season of aquatic insects (i.e., warm summer months when water temperatures promote fast larval growth; Sponseller et al., 2010). For example, flash floods can occur at any time in some desert streams, whereas in others, floods are more predictable and seasonal (Sabo and Post, 2008), and yet others have elements of both hydrologic regimes. Hydrology, the 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 anthropogenic alterations to hydrologic regime (i.e., flow regulation, channelization; Laeser et al., 2005; Paetzold et al., 2008). Along desert rivers, intermittent flow can affect the species composition, richness, abundance, and biomass of terrestrial arthropods (Hagen and Sabo, 2012; McCluney and Sabo, 2012). Variation in hydrologic regime will probably also affect terrestrial predators. Bats are an abundant and speciose group of terrestrial consumers along desert streams (Rogers et al., 2006; Williams et al., 2006) and depend on aquatic insects as food (Belwood and Fenton, 1976; Brigham et al., 1992). Bats in the Sonoran Desert are generally most active during the summer, coinciding with reproduction (May–August), and are relatively inactive for 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 (Hagen and Sabo, 2012), and variation in prey availability (Akasaka et al., 2009; Fukui et al., 2006). Further temporal variation in bat activity may be in response to changes in aquatic insect emergence (Fukui et al., 2006). Specifically, variation in aquatic insect life history characteristics, including timing of peak emergence and duration of emergence, may influence resource tracking by foraging bats.

Our purpose was to document and relate temporal variation in insect availability and bat activity along two Sonoran Desert streams with contrasting riparian vegetation and differing patterns of availability of aquatic and terrestrial prey. First, we described temporal patterns in insect availability by measuring aquatic insect emergence, and standing stocks of aquatic and terrestrial aerial insects (abundance and biomass). We then measured temporal patterns in bat activity to explore how interactions between bats and aquatic and terrestrial prey vary in streams with contrasting patterns of insect prey availability.

2. Methods

2.1. Study sites

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

Sycamore Creek is an intermittent stream with a coarse sand and gravel substratum that alternates between riffles and pools. Our study sites were in the Tonto National Forest between 1024 and 1036 m elevation. The 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. The stream is characterized by low and intermittent flows during the summer months and high and continuous flows in the winter. The majority of floods occur between December and April, with occasional, small flash floods between July and November (Fig. 1). Mean air temperature near the river was 15.5 °C during the study (Table 1). Stream width varied from 0 to 20 m and some sections of 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.). The limited gallery forest provides little shade. In addition to the sparse gallery forest, the riparian habitat includes some grassland.

Like Sycamore Creek, the San Pedro River is an intermittent stream with coarse sand and gravel substratum, and riffles and pools channel sections. Our study sites ranged between 603 and 610 m elevation and was in the San Pedro River Preserve. Unfortunately there is no gage downstream of our study site on the San Pedro River so long-term discharge data from USGS gages 09471000 (1904–2009, San Pedro River at Charleston, AZ) and 09473000 (1931–2009, 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 in the winter and dry season (October–June), while Aravaipa Creek discharge reflects local monsoon conditions. The watershed area of the study sites is approximately 12,000 km^2. The San Pedro River has 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. 1; Hirschboeck, 2009). Stream width varied from 0 to 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 (Table 1). The San Pedro River supports a dense closed canopy gallery forest, composed of Fremont cottonwood (*Populus fremontii*), Goodding willow, coyote willow (*Salix exigua*) and tamarisk (*Tamarix* sp.) trees. Riparian habitat is extensive along the San Pedro River consisting of grasslands and abandoned agricultural fields that have transitioned into grassland habitat. The floodplain is nested between gallery forest along the main channel and a band