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River food chains lead to riparian bats and birds in two mid-order rivers

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Abstract. River regulation can modify natural flow regimes with deleterious effects on aquatic communities. While the effects of flow manipulation on the physical environment and populations and assemblages of aquatic organisms have been described thoroughly, how and to what extent river regulation influences ecosystem processes like food web architecture is less studied. Emergent aquatic insect prey can provide an important food resource to riparian consumers like birds and bats with concomitant consequences for nutrient cycling through aquatic–terrestrial food webs, thus potentially increasing the spatial influence of river regulation into the riparian zone and beyond. We used naturally abundant stable isotopes of carbon and nitrogen to compare food web architecture (trophic position and reliance on an aquatic nutritional pathway) leading to birds and bats between a regulated river, the Tuolumne River downstream of Hetch Hetchy Reservoir, and an adjacent unregulated river, the Merced River, located in Yosemite National Park on the west slope of the Sierra Nevada, California, USA. We found that both birds and bats derived >50% of their nutrition from food webs originating in photosynthesis by algae. In addition, birds and bats occupied a similar trophic position to predatory fish in other systems. Both birds and bats seemed to rely more strongly on an aquatic nutritional pathway during the dryer year of our study period, underscoring the potential importance of emergent aquatic prey as a water subsidy in dry systems and in dry years. In the Tuolumne River, reservoir managers strive to simulate characteristics of the natural flow regime, including seasonal scouring flows and prolonged floodplain inundation. Although we found no conclusive evidence of an effect of river regulation on food web responses, our study suggests that nutrient cycling through aquatic–terrestrial food webs expands the potential influence of river regulation to organisms and ecosystems typically characterized as terrestrial.

Key words: aquatic–terrestrial food webs; food chain; Hetch Hetchy; Myotis yumanensis; precipitation; river regulation; stable isotopes; songbirds; trophic position; Yosemite National Park.

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INTRODUCTION

Dams reduce annual river runoff by 15% globally (Nilson et al. 2005), resulting in catchment-scale impacts that include upstream and downstream inundation, flow manipulation, and channel fragmentation. Flow manipulations in particular modify aquatic communities (Nilson et al. 2005) adapted to natural flow regimes (Poff et al. 1997). These effects have prompted attempts by land managers to replicate natural flow regimes and restore natural river processes (e.g., Chen and Olden 2017, Poff and Olden 2017). Most restoration efforts that focus on elements of ecosystem structure typically consider species diversity or population size of taxa of interest (Palmer and Febria 2012). However, describing these structural elements does not answer the question of why an ecosystem is in trouble. Furthermore, structural responses to environmental conditions do not always correlate with functional responses. Researchers have therefore begun to complement traditional studies of ecosystem structure by describing aspects of ecosystem function such as trophic networks and nutrient cycling (e.g., Bellmoore et al. 2017, Sullivan et al. 2018).

Dynamic processes such as river runoff and flooding deliver sediments, nutrients, and organic matter from upland and riparian zones to streams (Junk et al. 1989, Vannote et al. 1980). Nakano et al. (1999) identified the importance of prey items originating from the riparian zone for delivery to aquatic consumers; and Baxter et al. (2005) described the value of aquatic insects as prey for riparian consumers. Although river regulation can reduce the magnitude of emergent aquatic insect biomass and abundance (Jonsson et al. 2013, Kennedy et al. 2016), few studies have considered whether this reduced prey subsidy leads to a change in food web structure or nutrient cycling through riparian consumer organisms (but see Sullivan et al. 2018). Although the spatial extent of emergent aquatic insect dispersal can extend from meters to kilometers into the upland environment (Muehlbauer et al. 2014), riparian consumers like birds and bats may transport energy and nutrients derived from aquatic primary production much farther upland—and thereby increase the spatial envelope of stream ecosystems. Therefore, understanding nutrient cycling through highly mobile riparian consumers may expand our understanding of the spatial influence of river regulation on linked aquatic–terrestrial ecosystems.

Food chain length is a measure of food web architecture and is related to the complexity of trophic interactions leading to a top consumer (Sabo et al. 2009). Longer food chains tend to have more biodiversity and resilience to environmental changes (Pimm and Lawton 1977, Pimm 1984), though this depends on degree of omnivory, species richness, and individual life-history traits (Downing and Leibold 2010, Wootton and Stouffer 2016). Environmental controls on food chain length include ecosystem size, disturbance, and resource availability (Post 2002). Smaller ecosystems tend to have shorter food chains (Post 2002). Although river regulation increases inundation extent above dams (i.e., reservoirs), on the whole, river regulation reduces inundation extent by reducing discharge, resulting in decreased functional ecosystem size (Waddle and Holmquist 2013). Furthermore, in aquatic ecosystems, the functional attribute linking ecosystem size to food chain length tends to be flooding (Sabo et al. 2009, Sullivan et al. 2015, Jackson and Sullivan 2018), and regulated rivers generally have less frequent and lower magnitude floods than unregulated rivers (Poff et al. 1997). Reduction in flow variability and flood magnitude is associated with shorter food chains (Sabo et al. 2010, Takimoto and Post 2013, Jackson and Sullivan 2018). For example, in the Eel River in California, scouring floods tend to lengthen food chains by removing predator-resistant, late-successional taxa (e.g., armored caddisflies), which releases algae from grazing pressure and promotes secondary production by mobile early-successional taxa (e.g., mayflies) susceptible to predation (Power 1992, 1995, Power et al. 1995).

Stable isotope analysis is a valuable tool for revealing trophic position and diet (Collier et al. 2002, Hicks et al. 2005). The ratio of ^{13}C to ^{12}C (δ^{13}C) can vary between terrestrial and aquatic primary producers (Finlay 2001). This distinction is retained in consumer organism tissues (DeNiro and Epstein 1978) so that the source of the carbon (e.g., from stream algae or riparian deciduous shrubs) can be determined by comparing δ^{13}C of consumers to δ^{13}C of primary producers. In addition, nitrogen isotope signatures can resolve the trophic position of a consumer organism as there is, in general, a 3–4‰ enrichment of δ^{15}N (the ratio of ^{15}N to ^{14}N) with each trophic step (Post 2002).

We compared reliance on an aquatic nutritional pathway by, and trophic position of, riparian birds and bats between a regulated river system and an adjacent unregulated river, both located in Yosemite National Park on the western slope of the Sierra Nevada in California, USA. Recognizing the importance of interannual differences in precipitation to these systems, we also compared response metrics between a relatively wet year and a relatively dry year. We used trophic position of bats and birds as a comparative measure of food chain length. We predicted that birds and bats foraging within a regulated river system would rely less on an aquatic nutritional pathway and that river regulation would reduce food web complexity and therefore trophic position of riparian consumers. In addition, we predicted that these effects would be exaggerated in a relatively dry year.

Methods

Site description

We conducted this study on a regulated section of the Tuolumne River downstream of Hetch Hetchy Reservoir and on an unregulated section of the Merced River as part of an ongoing holistic study of the ecological impacts of river regulation. Dam operations have reduced annual peak discharges of the Tuolumne River by an estimated 35%, the duration of high flow periods by 40%, and average monthly discharge by 65% (McBain and Trush 2007, Russo et al. 2011). The Merced River is unregulated until downstream of the study section. The regional climate is Mediterranean-type and characterized by dry–wet seasonality and high interannual variability in precipitation (Dettinger et al. 2011). We conducted this study from 2016 to 2017. Mean daily discharge was 469% and 241% higher for the Tuolumne and Merced Rivers, respectively, in 2017 compared to 2016 (USGS 2018). Furthermore, 2016 was the last year of a multi-year drought that began in 2012 (Luo et al. 2017).

We focused our sampling efforts on the Tuolumne River in an area known as Poopenaut Valley, an approximately 0.25-km^2 floodplain meadow system situated 4 km downstream of O'Shaughnessy Dam at ~1000 m asl (Fig. 1). Poopenaut Valley provides important habitat for riparian taxa and is the largest riparian area in Yosemite National Park impacted by river regulation. We chose the Merced River as a reference study location because the climate is similar and the two watersheds drain parallel western aspects of the Sierra Nevada. There are two major differences between the rivers aside from regulation. Although unregulated, the Merced River has other infrastructure including riprap, bridges, roads, and other development. The Tuolumne River flows through wilderness until it reaches Hetch Hetchy Reservoir. In addition, the Merced River flows through the much larger floodplain meadow system of Yosemite Valley. We attempted to minimize the impact of the latter by sampling at two reaches approximately 10 km apart along the Merced River. We sampled at Yosemite Valley, a 15-km^2 floodplain meadow system located at ~1200 m asl; and farther downstream at the confluence of the Merced River and Cascade Creek—a 0.35-km^2 braided floodplain system located at ~1000 m asl (Fig. 1). We selected these reaches based on historic bat and bird surveys with a high rate of capture, as well as the existence of habitat elements such as composition and structure of riparian vegetation, channel-reach morphology, and bed composition similar to those found in the regulated study reach.

Sample collection

We captured bats in Poopenaut Valley (hereafter referred to as the regulated study reach) along the Tuolumne River and at the upper and lower unregulated study reaches along the Merced River over four separate sampling efforts (one or two nights per reach) in May, June, and September 2016, and in September 2017. We caught 16 bats across five sampling nights in May and June of 2016, compared to 53 over two sampling nights in September 2016. Therefore, we concentrated our 2017 effort in September and caught 68 bats over five sampling nights. We deployed multiple bat-specific mist nets (38 mm mesh) during each sampling effort including five or six single-high (three meter) nets and a single triple-high (10 m) net. We deployed nets over and along waterbodies including side-channels, oxbow ponds, and the main channel of the river to maximize capture success. We typically opened nets around dusk and closed them when we reached our target sampling number, temperatures dropped below 5°C, or capture rates diminished. We checked nets frequently to minimize escape and stress of captured bats (MacCarthy et al. 2006). After extracting bats, we

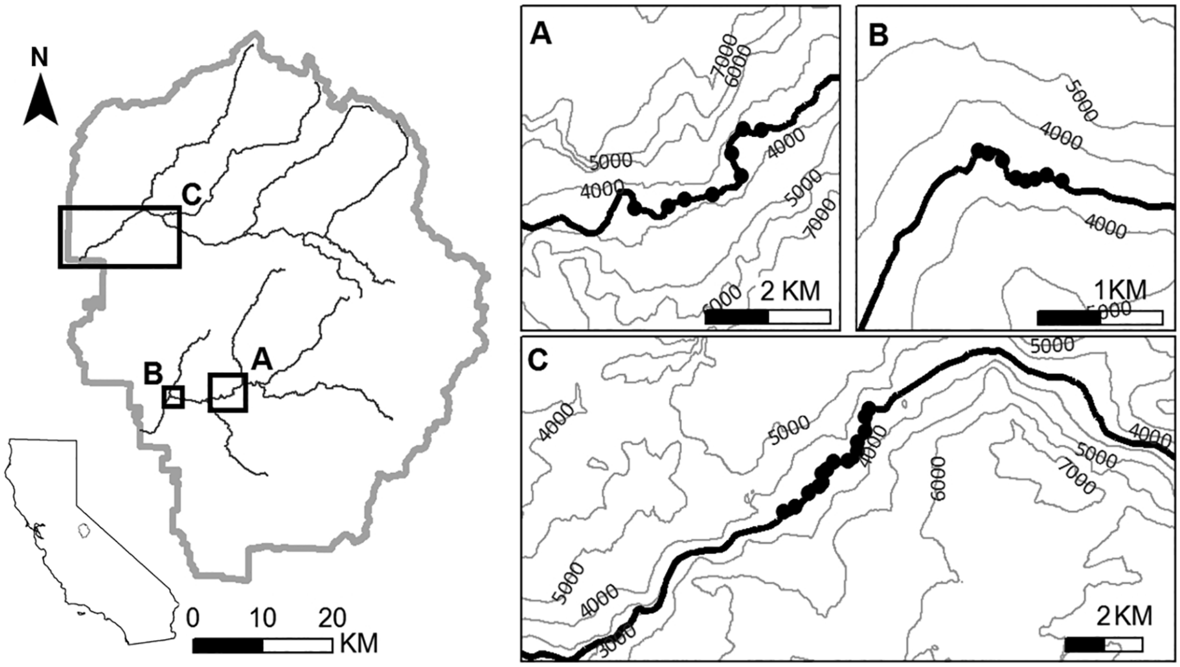

Fig. 1. Map of Yosemite National park and the study areas located at (A) unregulated upper, (B) unregulated lower, and (C) regulated. Within each study area, we collected epilithic algae and detritus from 8 to 13 sites along each river reach (black dots). The position of Yosemite National Park (latitude/longitude: 37.8, −119.5) in California is shown in the bottom left corner.

placed them individually in clean, disinfected cloth bags. We identified all captured bats to species.

For the morphologically cryptic but acoustically distinct species pair *Myotis yumanensis*/ *Myotis lucifugus*, when possible we confirmed species identification by the characteristic frequency of that bat's echolocation calls (Parsons and Szewczak 2009) recorded from tethered or hand-released flight (Weller et al. 2007). We recorded calls using a USB-powered ultrasonic microphone (Binary Acoustics Technology, Tucson, Arizona, USA, or Pettersson Elektronik AB, Uppsala, Sweden) connected to a Microsoft Surface Pro computer running SonoBatLIVE (SonoBat Software for Bat Call Analysis, Arcata, California, USA). Of the 49 recordings where we obtained a clean characteristic frequency, all confirmed our in-hand identification of *M. yumanensis*, with forearm lengths also consistent with this determination (Weller et al. 2007). We thus made the simplifying assumption that all other *yumanensis*/*lucifugus* samples were from *M. yumanensis*. Yosemite is within the range of *M. lucifugus*, and we have recorded *M. lucifugus* activity in both watersheds, although rarely. We therefore recognize that some of our *M. yumanensis* samples may include *M. lucifugus*.

From bats, we collected hair and blood samples. We used small blunt-end scissors to take two-to-three hair snips from the dorsal region (~30 mm^2). We stored hair samples in 0.5-mL microcentrifuge tubes containing silica desiccant beads. To determine whether a bat was a recaptured individual, we looked for missing fur left by fur sampling. We did not have any recaptures. We drew blood (approximately 10–50 μL) from the interfemoral vein using a sterile beveled syringe needle (27–29 ga, depending on bat size; Wimsatt et al. 2005) and collected the beaded blood into a 50-μL non-heparinized capillary tube for transfer to a 0.5-mL microcentrifuge tube containing 70% ethanol. It is important to mention that preservation of blood samples in ethanol can lead to fractionalization of stable isotopes compared to dried or frozen samples (e.g., Bugoni et al. 2008). We used bat weights to determine maximum blood sample volume, with a target of no more than 0.5–1% of the individual animal's body weight (6–10 µL/g), in accordance with recommended maximum sample volume (Sikes 2016). We conducted all bat capturing, handling, and processing in accordance with methods described by Kunz et al. (2009) and the most current White Nose Syndrome decontamination protocol available at the time (USFWS 2016).

We captured birds at the regulated study reach and the upper unregulated study reach over five separate sampling efforts (1–2 mornings per reach)—spring (April–June) 2016; summer (late-July) 2016; fall (September) 2016; and spring (May–early July) 2017. We captured birds at the lower unregulated study reach in September 2016 only. We used species-specific playbacks to target captures of the most commonly occurring riparian-associated breeding species: warbling vireo (*Vireo gilvus*), yellow warbler (*Setophaga petechia*), song sparrow (*Melospiza melodia*), and black-headed grosbeak (*Pheucticus melanocephalus*). We also collected samples from incidental captures of species with similar life-history traits or feeding ecology. We identified each bird to species, and applied a uniquely numbered band, according to standard protocols (Ralph et al. 1993, Owen 2011).

From birds, we collected feather and blood samples. We collected approximately two-to-four breast feathers from each bird and stored them in key envelopes containing desiccant beads. We drew blood (approximately 10–50 µL) from the brachial vein located on the ventral side of the humeral-radial-ulnar joint. We punctured the vein using a 26-ga beveled syringe needle and collected the blood in a 50-µL non-heparinized capillary tube for transfer to a 0.5-mL microcentrifuge tube containing 70% ethanol. Blood samples were, at most, 0.6% of the bird's total body weight, well below the maximum 1% of total body weight recommended (Owen 2011). When we captured an individual more than once, we took tissue samples each time if captures were more than 10 d apart; however, recognizing that whole blood turnover occurs over ~26–44 d depending on animal mass (Thomas and Crowther 2015, Vander Zanden et al. 2015), we only used the most recent blood sample for analysis.

We collected blood samples from 127 individual bats belonging to eight species, and hair samples from 115 individual bats belonging to eight species across both years and all sampling sites. We collected blood samples from 146 individual birds belonging to 27 species, and feather samples from 141 individual birds belonging to 26 species across both years and all sampling sites. Target species comprised 90 independent blood samples, including song sparrow (35), black-headed grosbeak (27), warbling vireo (22), and yellow warbler (6), and non-target species comprised 56 samples. Only song sparrow, black-headed grosbeak, and warbling vireo had a sufficient sample size to warrant comparison between study systems. Because we only collected birds from the lower unregulated site in the fall, we eliminated birds captured from this site from our comparison between study systems and focused on birds captured during the breeding season.

We collected epilithic algae and stream-conditioned leaf litter (i.e., detritus) from upstream, mid-reach, and downstream locations along each study reach to use as basal resources (~10 samples per study reach; Fig. 1). We used stream-conditioned leaf litter rather than green terrestrial plants to holistically represent the riparian plant community (Finlay 2001). We recognize that detritus likely underwent some microbial processing prior to uptake into the food web by consumers and this may have led to a small ^{13}C-enrichment (Finlay 2001). We also opportunistically collected spiders belonging to the family Tetragnathidae along all three study reaches (n = 21). Tetragnathids build their webs directly adjacent to or spanning waterways to feed opportunistically on emergent aquatic insects making them an ideal riparian consumer to compare with birds and bats which have been less well-studied. Therefore, we used tetragnathid metrics to confirm the validity of our methods. All algae, detritus, and tetragnathids were collected in early August of 2016 and 2017 and stored in 70% ethanol.

Sample processing

We freeze-dried blood, hair, and feather samples from bats and birds and entire bodies of tetragnathids in the laboratory. We ground tetragnathids (one-to-three individuals per sample) into a fine powder using a mortar and pestle.

We then packed a small amount of each composite sample into tin capsules. After freeze-drying, blood samples were sufficiently homogenous and powdery for packing into tin capsules, and we packed one-to-three entire feathers and entire hair samples into tin capsules. We sorted epilithic algae and detritus from other materials and rinsed the samples with distilled water. After oven-drying at 60°C for 24–48 h, we homogenized epilithic algae and detritus into a fine powder using a Pica Blender Mill (Cianflone Scientific Instruments Corporation, Pittsburgh, Pennsylvania, USA) or mortar and pestle before packing samples into tin capsules for analysis. Mean sample size was 0.63 ± 0.09 mg (SD) for tetragnathids, 0.53 ± 0.13 mg for bat blood, 0.59 ± 0.16 mg for bird blood, 0.53 ± 0.11 mg for bat hair, 0.63 ± 0.12 mg for bird feathers, 1.27 ± 0.13 mg for algae, and 3.34 ± 0.16 mg for detritus.

We used continuous-flow isotope-ratio mass spectrometry (EA-IRMS) to determine $\delta^{13}C$ and $\delta^{15}N$ for all samples at Washington State University's Stable Isotope Core (Pullman, Washington, USA). We reported results in δ (‰) notation defined as: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$ where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ for the sample or standard with Vienna Pee Dee Belemite as the standard for C and atmospheric N^2 as the standard for N. Delta values were calculated using a multi-point normalization by fitting a regression line through the running standards (acetanilide, yeast, and keratin). Typical analytical precision was <0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ determination.

Analytical methods

After processing, we used the two-source food web model from Post (2002) to estimate bat, bird, and spider trophic position; $TP = \lambda + \{\delta_c - [\delta_{b1} \times \alpha + \delta_{b2} \times (1 - \alpha)]\}/\Delta_n$ where λ is the trophic position of the basal food sources (i.e., 1 for primary producers); δ_c is the $\delta^{15}N$ signature of the consumer; δ_{b1} and δ_{b2} are the signatures of the two basal food sources; α is the proportion of N from basal food source one; and Δ_n is the enrichment in $\delta^{15}N$ per trophic level (i.e., 3.4‰; Post 2002). We used a two-end-member Bayesian isotopic mixing model to determine the proportion of N derived from basal source 1 (i.e., α) with the R software package simmr (Stable Isotope Mixing Models in R; Parnell and Inger 2019).

Epilithic algae and detritus were the basal food source end members. We used $\delta^{13}C$ and $\delta^{15}N$ data to estimate the contribution from each food source to the consumer. We estimated trophic discrimination factors for bats, birds, and spiders using the per-trophic-step discrimination described in Post (2002; i.e., 3.4‰ ± 0.98‰ for $\delta^{15}N$ and 0.39‰ ± 1.3‰ for $\delta^{13}C$) multiplied by the estimated number of trophic transfers between the consumer and basal resources (estimated a priori as the difference between the consumer $\delta^{15}N$ and mean basal resource $\delta^{15}N$ divided by 3.4‰), which is consistent with other aquatic food web investigations (e.g., McHugh et al. 2010, Sullivan et al. 2015). It is important to note that recent studies have questioned the use of a single, fixed trophic discrimination factor (TDF; Caut et al. 2009, Martinez del Rio et al. 2009). However, Vanderklift and Ponsard (2003) found that TDF for $\delta^{15}N$ in blood and feathers of birds, blood and hair of mammals, and whole bodies of insects were indistinguishable. In the absence of laboratory-derived TDF estimates for our specific taxa and tissues, we decided to use the TDF suggested by Post (2002) which allowed us to directly compare our results to many previous studies. The Post (2002) $\delta^{15}N$ TDF is within one standard deviation of several laboratory-based estimates found in the literature for insectivorous bats and songbirds (e.g., 2.6‰ ± 0.09‰ for *Myotis myotis* hair; Siemers et al. 2011, Frick et al. 2014; and 1.8–2.7‰ for *Setophaga coronata* blood Pearson et al. 2003). The $\delta^{13}C$ TDF suggested by Post (2002) is low compared to laboratory-based TDF (e.g., 3.6‰ ± 0.28‰ for *Myotis myotis* hair, Siemers et al. 2011; and 1.5–2.2‰ for *Setophaga coronata* blood, Pearson et al. 2003). We expect ^{13}C discrimination in animals feeding at a higher trophic position to be disproportionately affected by using a lower estimate of TDF for $\delta^{13}C$ (Ben-David and Flaherty 2012). To evaluate the ramifications of this effect, we also estimated reliance on aquatically derived nutrition using taxa- and tissue-specific diet-dependent discrimination factors (DDDF) for $\delta^{13}C$ derived from Caut et al. (2009; 0.72 ± 0.58 for bat blood, 1.63 ± 0.62 for bat hair, 0.86 ± 0.25 for bird blood, 2.16 ± 0.35 for bird feathers, and 0.94 ± 0.15 for spiders) and taxa-specific TDF derived from the literature (3 ± 0.5 for bats, 2 ± 0.5 for birds, and 1 ± 0.5 for spiders; Pearson et al. 2003, Siemers et al. 2011, Frick et al. 2014, Kautza and Sullivan 2016). We then compared these estimates to those using Post (2002) TDF.

We determined mean, standard deviation, minimum, and maximum values of $\delta^{13}C$ and $\delta^{15}N$ for epilithic algae, detritus, spiders, bats, and birds. We used $\delta^{13}C$ and $\delta^{15}N$ of blood samples to reflect dietary trends on the scale of one-to-two months (Thomas and Crowther 2015, Vander Zanden et al. 2015) and $\delta^{13}C$ and $\delta^{15}N$ of hair and feather samples to reflect longer-term dietary trends. We visually inspected stable isotope signatures of blood collected from each taxonomic group and basal resources using a bi-plot of $\delta^{13}C$ and $\delta^{15}N$. We compared $\delta^{13}C$ and $\delta^{15}N$ of blood collected from bats and birds between study sites and years using ANOVA and followed this with Tukey's HSD to identify differences between pairs. We also used ANOVA to compare reliance on an aquatic nutritional pathway and trophic position of Yuma myotis between sites and years. We determined whether short-term individual dietary trends of bats and birds were correlated with long-term individual dietary trends within each site using ANCOVA followed by linear regression. We used a step-down technique to identify the most parsimonious model by comparing AIC values among models (Crawley 2007). We considered the most parsimonious model within 2 AIC units from the full saturated model to be the best model (Crawley 2007). We log-transformed data to meet assumptions of normal distribution and homogeneity of variance when appropriate. We had insufficient sample size to include season in our analysis, so for all comparisons between study systems, we only considered birds captured during the breeding season (May to early July) and bats captured in September.

RESULTS

There was sufficient separation between $\delta^{13}C$ values of epilithic algae and detritus at the regulated and lower unregulated study reaches to use them in our mixing models; however, epilithic algae and detritus $\delta^{13}C$ signatures overlapped significantly at the upper unregulated study reach (Fig. 2). Therefore, we only estimated riparian consumer reliance on an aquatic energetic pathway and trophic position at the regulated and lower unregulated reaches. We did not sample any birds at the lower unregulated study reach during the breeding season; therefore, we were unable to compare reliance on an aquatic nutritional pathway by breeding birds between systems.

Among the three taxa, bats exhibited the highest $\delta^{13}C$ and $\delta\ ^{15}N$, followed by birds, then tetragnathids across all years and sites (Fig. 2; Appendix S1: Tables S1, S2, S3, and S4). $\delta^{13}C$ in Yuma myotis blood was significantly lower at the regulated study reach (−22.68 ± 1.64) compared with either of the unregulated study reaches (unregulated upper − 24.28 ± 1.15; unregulated lower −23.16 ± 1.89; $F = 5.40$, $P = 0.006$; Appendix S1: Table S5, Fig. S1), but did not differ between years and the interaction term was also insignificant (Appendix S1: Table S5, Fig. S1). $\delta^{15}N$ in Yuma myotis blood did not differ between sites or years (Appendix S1: Table S5, Fig. S1). $\delta^{13}C$ in song sparrow and black-headed grosbeak blood did not differ between sites or years (Appendix S1: Table S5, Fig. S2). $\delta^{15}N$ in black-headed grosbeak blood was lower in 2017 (4.66 ± 0.92) compared to 2016 (5.61 ± 0.62; $F = 7.47$, $P = 0.013$; Appendix S1: Table S5, Fig. S2), but did not differ between sites. Song sparrow blood $\delta^{15}N$ was significantly higher at the regulated reach (6.19 ± 0.28) compared to the upper unregulated reach (5.07 ± 0.34; $F = 24.44$, $P < 0.001$; Appendix S1: Table S5, Fig. S2), and the interaction term between site and year was also significant ($F = 5.11$, $P = 0.040$; Appendix S1: Table S5, Fig. S2). Warbling vireo blood $\delta^{13}C$ was significantly higher in 2016 (−23.33 ± 0.54) compared with 2017 (−23.91 ± 0.30; $F = 7.37$, $P = 0.014$; Appendix S1: Table S5, Fig. S2); however, $\delta^{13}C$ differences <1‰ are typically not ecologically meaningful. $\delta^{15}N$ of warbling vireo blood did not differ between sites or years (Appendix S1: Table S5, Fig. S2).

For Yuma myotis, $\delta^{13}C$ and $\delta^{15}N$ in blood and hair were positively correlated (Appendix S1: Fig. S3); however, both the slopes and intercepts at each study location differed (Appendix S1: Table S6, Fig. S3). For song sparrow, blood and feather samples were also correlated with respect

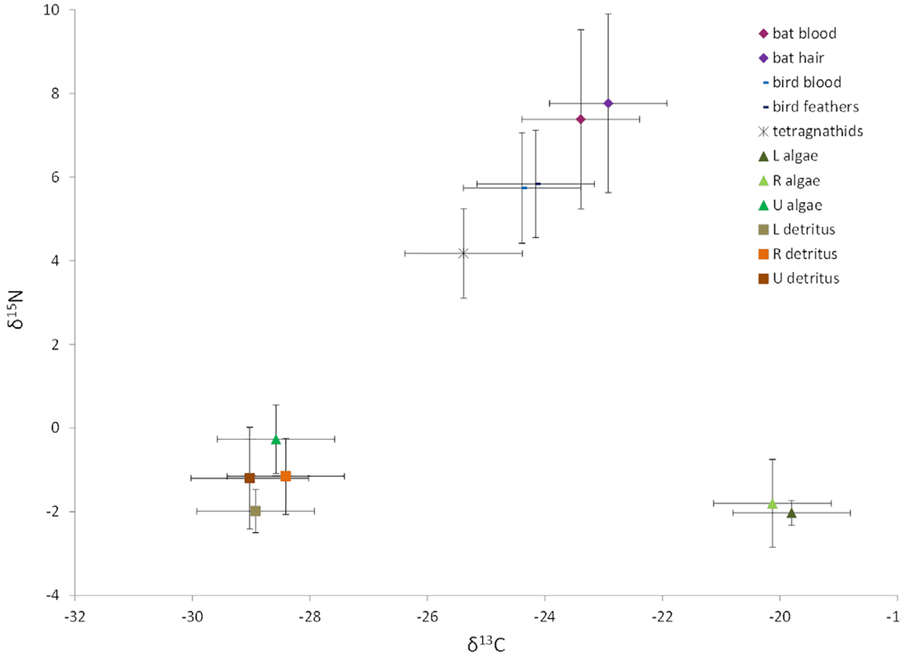

Fig. 2. Bi-plot of $\delta^{13}C$ and $\delta^{15}N$ for bats, birds, spiders (tetragnathids), epilithic algae, and detritus. Sites are represented as (L) lower unregulated, (R) regulated, and (U) upper unregulated.

to $\delta^{13}C$ but not $\delta^{15}N$, and this was unrelated to study site (Appendix S1: Table S6, Fig. S3A, B, C, and D). For black-headed grosbeak, $\delta^{13}C$ and $\delta^{15}N$ in blood and feathers were unrelated to each other (Appendix S1: Table S6, Fig. S4C, D, G, and H). Due to insufficient sample sizes, we omitted warbling vireo and yellow warbler from this analysis.

Our estimates of reliance on an aquatic energetic pathway using taxa- and tissue-specific DDDF and taxa-specific TDF were within one standard deviation of estimates derived using Post (2002) TDF (Appendix S1: Table S7). Hereafter, we report estimates derived using Post (2002). Among bats, mean reliance on an aquatic energetic pathway estimated from blood samples ranged from 0.61 (long-eared myotis, $n = 1$) to 0.82 ± 0.09 (SD; Yuma myotis, $n = 95$; Table 1), and mean trophic position ranged from 2.38 (big brown bat, $n = 1$) to 3.59 ± 0.70 (Yuma myotis, $n = 95$; Table 2). Mean reliance on an aquatic energetic pathway by riparian bird species estimated from blood samples ranged from 0.61 (MacGillivray's warbler, $n = 1$) to 0.67 ± 0.09 (song sparrow, $n = 26$; Table 1), and mean trophic position ranged from 2.17 (black-throated gray warbler, $n = 1$) to 4.16 (Brewer's sparrow, $n = 1$; Table 2). Mean tetragnathid trophic position was 2.66 ± 0.32, and their reliance on an aquatic energetic pathway was 0.57 ± 0.07 (Tables 1 and 2). Estimates of trophic position and consumer reliance on an aquatic energetic pathway estimated from hair and feather samples are reported in Tables 3 and 4 along with estimates from all species collected.

Yuma myotis relied more heavily on an aquatic energetic pathway in 2016 (0.82 ± 0.09) compared to 2017 (0.80 ± 0.10; $F = 3.36$, $P = 0.070$), and this difference was primarily attributable to more variable and overall decreased reliance on primary production by algae at the lower unregulated site in 2017 (2016 0.84 ± 0.08; 2017 0.78 ± 0.11; $F = 5.90$, $P = 0.017$; Fig. 3; Appendix S1: Table S5). Trophic position of Yuma myotis did not differ between sites (unregulated lower 3.62 ± 0.76; regulated 3.56 ± 0.64; $F = 0.07$, $P = 0.786$) or years (2016 3.65 ± 0.74; 2017 3.52 ± 0.65; $F = 1.06$, $P = 0.307$), and the interaction term was also insignificant ($F = 1.87$, $P = 0.175$; Fig. 3, Appendix S1: Table S5).

Table 1. Riparian consumer reliance on an aquatic nutritional pathway estimated from blood or whole-body samples.

Taxonomic name	Common name	*n*	Mean	SD	Min.	Max.
Songbirds						
Melospiza melodia	**Song sparrow**	26	0.67	0.09	0.5	0.85
Vireo gilvus	**Warbling vireo**	21	0.67	0.08	0.53	0.81
Pheucticus melanocephalus	**Black-headed grosbeak**	16	0.63	0.07	0.49	0.79
Vermivora celata	Orange-crowned warbler	9	0.53	0.09	0.36	0.65
Melospiza lincolnii	Lincoln's sparrow	8	0.71	0.07	0.61	0.82
Setophaga petechia	**Yellow warbler**	6	0.62	0.09	0.47	0.73
Dendroica coronata	Yellow-rumped warbler	4	0.66	0.03	0.62	0.70
Passerina amoena	Lazuli bunting	3	0.49	0.03	0.45	0.51
Troglodytes aedon	House wren	3	0.77	0.01	0.76	0.77
Vireo cassinii	Cassin's vireo	3	0.71	0.01	0.69	0.72
Contopus sordidulus	Western wood-pewee	2	0.73	0.01	0.73	0.74
Pipilo maculatus	Spotted towhee	2	0.63	0.09	0.56	0.69
Cardellina pusilla	Wilson's warbler	1	0.45	...	...	...
Carduelis pinus	Pine siskin	1	0.78	...	...	...
Geothlypis tolmiei	MacGillivray's warbler	1	0.61	...	...	...
Geothlypis trichas	Common yellowthroat	1	0.77	...	...	...
Icterus bullockii	Bullock's oriole	1	0.70	...	...	...
Phalaenoptilus nuttallii	Common poorwill	1	0.63	...	...	...
Piranga ludoviciana	Western tanager	1	0.64	...	...	...
Setophaga nigrescens	Black-throated gray warbler	1	0.53	...	...	...
Spizella breweri	Brewer's sparrow	1	0.92	...	...	...
Turdus migratorius	American robin	1	0.68	...	...	...
Zonotrichia leucophrys	White-crowned sparrow	1	0.64	...	...	...
Agelaius phoeniceus	Red-winged blackbird	0	...	...	...	...
Cinclus mexicanus	American dipper	0	...	...	...	...
Euphagus cyanocephalus	Brewer's blackbird	0	...	...	...	...
Junco hyemalis	Dark-eyed junco	0	...	...	...	...
Bats						
Myotis yumanensis	**Yuma myotis**	95	0.82	0.09	0.66	0.98
Myotis californicus	California myotis	4	0.72	0.02	0.70	0.75
Myotis thysanodes	Fringed myotis	2	0.75	0.12	0.66	0.83
Eptesicus fuscus	Big brown bat	1	0.65	...	...	...
Lasionycteris noctivagans	Silver-haired bat	1	0.72	...	...	...
Myotis evotis	Western long-eared bat	1	0.61	...	...	...
Parastrellus hesperus	Canyon bat	1	0.62	...	...	...
Tadarida brasiliensis	Mexican free-tailed bat	1	0.67	...	...	...
Invertebrates						
Tetragnathidae		21	0.57	0.07	0.48	0.74

Notes: Number of samples (*n*), mean, standard deviation (SD), minimum (Min.), and maximum (Max.) values are presented. Data are shown by taxa and are inclusive of all years. Species in bold are the riparian focal species chosen for this study. Only those animals caught at either the regulated or unregulated lower study reaches are included. Tetragnathidae values are derived from samples that included their entire bodies. We use '...' to indicate when data was not available for that taxa.

DISCUSSION

We compared aquatic–terrestrial food webs leading to riparian birds and bats between a regulated river system and an unregulated river system over two years—one wet and one dry. We found significant overlap between $\delta^{13}C$ signatures for epilithic algae and terrestrially derived detritus, which limited estimation of trophic responses at one of the unregulated reaches and our ability to make comparisons between systems in birds (Fig. 2). However, we obtained preliminary evidence that bats and some birds relied more strongly on an aquatic nutritional pathway during the dry year. Furthermore, we observed that birds and bats foraging along both rivers are highly

Table 2. Riparian consumer trophic position estimated from blood or whole-body samples.

Taxonomic name	Common name	*n*	Mean	SD	Min.	Max.
Songbirds						
Melospiza melodia	**Song sparrow**	26	3.03	0.22	2.55	3.53
Vireo gilvus	**Warbling vireo**	21	2.89	0.27	2.21	3.29
Pheucticus melanocephalus	**Black-headed grosbeak**	16	2.77	0.32	2.07	3.24
Vermivora celata	Orange-crowned warbler	9	2.39	0.41	1.70	3.06
Melospiza lincolnii	Lincoln's sparrow	8	3.03	0.16	2.79	3.25
Setophaga petechia	**Yellow warbler**	6	2.79	0.21	2.49	3.10
Dendroica coronata	Yellow-rumped warbler	4	2.75	0.10	2.63	2.87
Passerina amoena	Lazuli bunting	3	2.37	0.05	2.31	2.41
Troglodytes aedon	House wren	3	3.26	0.02	3.25	3.28
Vireo cassinii	Cassin's vireo	3	3.05	0.05	3.00	3.11
Contopus sordidulus	Western wood-pewee	2	3.11	0.02	3.09	3.12
Pipilo maculatus	Spotted towhee	2	2.84	0.01	2.83	2.85
Cardellina pusilla	Wilson's warbler	1	2.03	…	…	…
Carduelis pinus	Pine siskin	1	3.26	…	…	…
Geothlypis tolmiei	MacGillivray's warbler	1	2.73	…	…	…
Geothlypis trichas	Common yellowthroat	1	3.24	…	…	…
Icterus bullockii	Bullock's oriole	1	2.95	…	…	…
Phalaenoptilus nuttallii	Common poorwill	1	2.82	…	…	…
Piranga ludoviciana	Western tanager	1	2.77	…	…	…
Setophaga nigrescens	Black-throated gray warbler	1	2.17	…	…	…
Spizella breweri	Brewer's sparrow	1	4.16	…	…	…
Turdus migratorius	American robin	1	2.96	…	…	…
Zonotrichia leucophrys	White-crowned sparrow	1	2.89	…	…	…
Agelaius phoeniceus	Red-winged blackbird	0	…	…	…	…
Cinclus mexicanus	American dipper	0	…	…	…	…
Euphagus cyanocephalus	Brewer's blackbird	0	…	…	…	…
Junco hyemalis	Dark-eyed junco	0	…	…	…	…
Bats						
Myotis yumanensis	**Yuma myotis**	95	3.59	0.70	2.92	6.50
Myotis californicus	California myotis	4	3.09	0.04	3.06	3.13
Myotis thysanodes	Fringed myotis	2	3.10	0.49	2.75	3.44
Eptesicus fuscus	Big brown bat	1	2.38	…	…	…
Lasionycteris noctivagans	Silver-haired bat	1	3.00	…	…	…
Myotis evotis	Western long-eared bat	1	2.75	…	…	…
Parastrellus hesperus	Canyon bat	1	2.63	…	…	…
Tadarida brasiliensis	Mexican free-tailed bat	1	2.75	…	…	…
Invertebrates						
Tetragnathidae		21	2.66	0.32	2.24	3.23

Notes: Number of samples (*n*), mean, standard deviation (SD), minimum (Min.), and maximum (Max.) values are presented. Data are shown by taxa and are inclusive of all years. Species in bold are the riparian focal species chosen for this study. Only those animals caught at either the regulated or unregulated lower study reaches are included. Tetragnathidae values are derived from samples that included their entire bodies. We use '...' to indicate when data was not available for that taxa.

reliant on an aquatic nutritional pathway, and food chains leading to birds and bats are comparable in length to other stream-riparian food chains. Although we were unable to provide clear evidence of an effect of river regulation on food web architecture leading to birds and bats, we observed that bats depended more on an aquatic nutritional pathway in the dryer year but only along the unregulated river (Fig. 3, Appendix S1: Table S5).

Comparison between the regulated and unregulated rivers and between years

Regulated river hydrology can alter both functional and structural components of river and riparian ecosystems (Poff and Zimmerman 2010,

Table 3. Riparian consumer reliance on an aquatic nutritional pathway estimated from hair or feather samples.

Taxonomic name	Common name	*n*	Mean	SD	Min.	Max.
Songbirds						
Melospiza melodia	**Song sparrow**	26	0.67	0.13	0.43	0.89
Pheucticus melanocephalus	**Black-headed grosbeak**	17	0.77	0.11	0.56	0.92
Vireo gilvus	**Warbling vireo**	17	0.82	0.10	0.57	0.93
Melospiza lincolnii	Lincoln's sparrow	7	0.76	0.11	0.56	0.89
Vermivora celata	Orange-crowned warbler	7	0.61	0.11	0.39	0.73
Setophaga petechia	**Yellow warbler**	4	0.72	0.02	0.70	0.74
Carduelis pinus	Pine siskin	2	0.86	0.03	0.84	0.88
Contopus sordidulus	Western wood-pewee	2	0.95	0.01	0.94	0.96
Dendroica coronata	Yellow-rumped warbler	2	0.75	0.17	0.63	0.87
Pipilo macalatus	Spotted towhee	2	0.76	0.00	0.76	0.76
Troglodytes aedon	House wren	2	0.73	0.05	0.69	0.76
Turdus migratorius	American robin	2	0.70	0.05	0.66	0.74
Vireo cassinii	Cassin's vireo	2	0.67	0.06	0.63	0.71
Cinclus mexicanus	American dipper	1	0.90	...	...	...
Geothlypis tolmiei	MacGillivray's warbler	1	0.71	...	...	...
Geothlypis trichas	Common yellowthroat	1	0.81	...	...	...
Icterus bullockii	Bullock's oriole	1	0.94	...	...	...
Phalaenoptilus nuttallii	Common poorwill	1	0.76	...	...	...
Piranga ludoviciana	Western tanager	1	0.87	...	...	...
Setophaga nigrescens	Black-throated gray warbler	1	0.60	...	...	...
Spizella breweri	Brewer's sparrow	1	0.94	...	...	...
Zonotrichia leucophrys	White-crowned sparrow	1	0.70	...	...	...
Agelaius phoeniceus	Red-winged blackbird	0	...	...	...	...
Euphagus cyanocephalus	Brewer's blackbird	0	...	...	...	...
Junco hyemalis	Dark-eyed junco	0	...	...	...	...
Passerina amoena	Lazuli bunting	0	...	...	...	...
Bats						
Myotis yumanensis	**Yuma myotis**	100	0.85	0.07	0.68	0.98
Myotis californicus	California myotis	5	0.79	0.04	0.74	0.84
Lasionycteris noctivagans	Silver-haired bat	2	0.90	0.02	0.88	0.91
Myotis thysanodes	Fringed myotis	2	0.81	0.13	0.71	0.90
Eptesicus fuscus	Big brown bat	1	0.79	...	...	...
Myotis evotis	Western long-eared bat	1	0.70	...	...	...
Parastrellus hesperus	Canyon bat	1	0.72	...	...	...
Tadarida brasiliensis	Mexican free-trailed bat	1	0.72	...	...	...

Notes: Number of samples (*n*), mean, standard deviation (SD) minimum (Min.), and maximum (Max.) values are presented. Data are shown by taxa and are inclusive of all years. Species in bold are the riparian focal species chosen for this study. Only those animals caught at either the regulated or unregulated lower study reaches are included. We use '...' to indicate when data was not available for that taxa.

Kennedy et al. 2016), but aquatic–terrestrial food web linkages are less studied (Dynesius and Nilsson 1994). Regulated river systems export lower quantities (biomass) of emergent aquatic insects to adjacent upland forests, particularly during peak emergence (Jonsson et al. 2013). This has been attributed to reduced magnitude and frequency of floods, and reduced flow throughout the year (Jonsson et al. 2013). In addition, the magnitude of emergent insect subsidies at the landscape scale depends on the proportion of lentic versus lotic habitat (Bartrons et al. 2013). Aquatic invertebrate production is generally higher in streams than in lakes, so turning lotic habitat into lentic habitat may in itself reduce emergence (Gratton and Vander Zanden 2009). River regulation may also create temporal asynchrony between breeding cycles of birds and bats with emergence events (Carey 2009). Therefore, we expected to observe greater reliance on an aquatic nutritional pathway in the unregulated river system. However, we were limited in our ability to test this hypothesis and what analyses we performed indicated greater reliance on an

Table 4. Riparian consumer trophic position estimated from hair or feather samples.

Taxonomic name	Common name	*n*	Mean	SD	Min.	Max.
Songbirds						
Melospiza melodia	**Song sparrow**	26	3.00	0.39	2.24	3.78
Pheucticus melanocephalus	**Black-headed grosbeak**	17	3.30	0.47	2.65	4.13
Vireo gilvus	**Warbling vireo**	17	3.53	0.48	2.39	4.34
Melospiza lincolnii	Lincoln's sparrow	7	3.29	0.36	2.71	3.83
Vermivora celata	Orange-crowned warbler	7	2.63	0.28	2.24	3.10
Setophaga petechia	**Yellow warbler**	4	3.04	0.04	2.99	3.07
Carduelis pinus	Pine siskin	2	3.49	0.02	3.47	3.51
Contopus sordidulus	Western wood-pewee	2	4.86	0.36	4.60	5.11
Dendroica coronata	Yellow-rumped warbler	2	3.09	0.68	2.61	3.58
Pipilo macalatus	Spotted towhee	2	3.22	0.02	3.20	3.23
Troglodytes aedon	House wren	2	2.93	0.33	2.69	3.16
Turdus migratorius	American robin	2	2.93	0.19	2.80	3.07
Vireo cassinii	Cassin's vireo	2	2.80	0.13	2.71	2.89
Cinclus mexicanus	American dipper	1	3.84			
Geothlypis tolmiei	MacGillivray's warbler	1	2.84	...	...	...
Geothlypis trichas	Common yellowthroat	1	3.30	...	...	...
Icterus bullockii	Bullock's oriole	1	4.39	...	...	...
Phalaenoptilus nuttallii	Common poorwill	1	3.14	...	...	...
Piranga ludoviciana	Western tanager	1	3.66	...	...	...
Setophaga nigrescens	Black-throated gray warbler	1	2.43	...	...	...
Spizella breweri	Brewer's sparrow	1	4.49	...	...	...
Zonotrichia leucophrys	White-crowned sparrow	1	3.00	...	...	...
Agelaius phoeniceus	Red-winged blackbird	0	...	...	...	...
Euphagus cyanocephalus	Brewer's blackbird	0	...	...	...	...
Junco hyemalis	Dark-eyed junco	0	...	...	...	...
Passerina amoena	Lazuli bunting	0	...	...	...	...
Bats						
Myotis yumanensis	**Yuma myotis**	100	3.73	0.70	2.91	6.40
Myotis californicus	California myotis	5	3.25	0.11	3.12	3.42
Lasionycteris noctivagans	Silver-haired bat	2	3.84	0.21	3.70	3.99
Myotis thysanodes	Fringed myotis	2	3.37	0.71	2.87	3.87
Eptesicus fuscus	Big brown bat	1	3.01	...	...	...
Myotis evotis	Western long-eared bat	1	2.79	...	...	...
Parastrellus hesperus	Canyon bat	1	2.87	...	...	...
Tadarida brasiliensis	Mexican free-trailed bat	1	2.99	...	...	...

Notes: Number of samples (*n*), mean, standard deviation (SD), minimum (Min.), and maximum (Max.) values are presented. Data are shown by taxa and are inclusive of all years. Species in bold are the riparian focal species chosen for this study. Only those animals caught at either the regulated or unregulated lower study reaches are included. We use '...' to indicate when data was not available for that taxa.

aquatic nutritional pathway by bats in the regulated river system, but only in the relatively wet year (Fig. 3, Appendix S1: Table S5).

Yuma myotis relied more on an aquatic nutritional pathway in 2016 compared to 2017 at the unregulated site (Fig. 3). In addition, δ^{3}C values for warbling vireo were higher relative to detritus values in 2016 compared to 2017 (Appendix S1: Table S5, Fig. S2), indicating greater reliance by both species on an aquatic nutritional pathway in 2016. Riparian consumers are known to respond more strongly to water subsidies in dry systems and dry seasons compared to wet systems and wet seasons (Allen et al. 2014). Therefore, birds and bats may preferentially consume emergent aquatic insects in dryer years and dryer systems in response to the water subsidy (i.e., in the bodies of their prey) as much as the prey subsidy. The importance of a prey subsidy is often mediated by the availability of in situ prey (Marczak et al. 2007), and terrestrial invertebrate abundance may have been diminished in the dryer year. Alternatively, scouring flows in both systems in

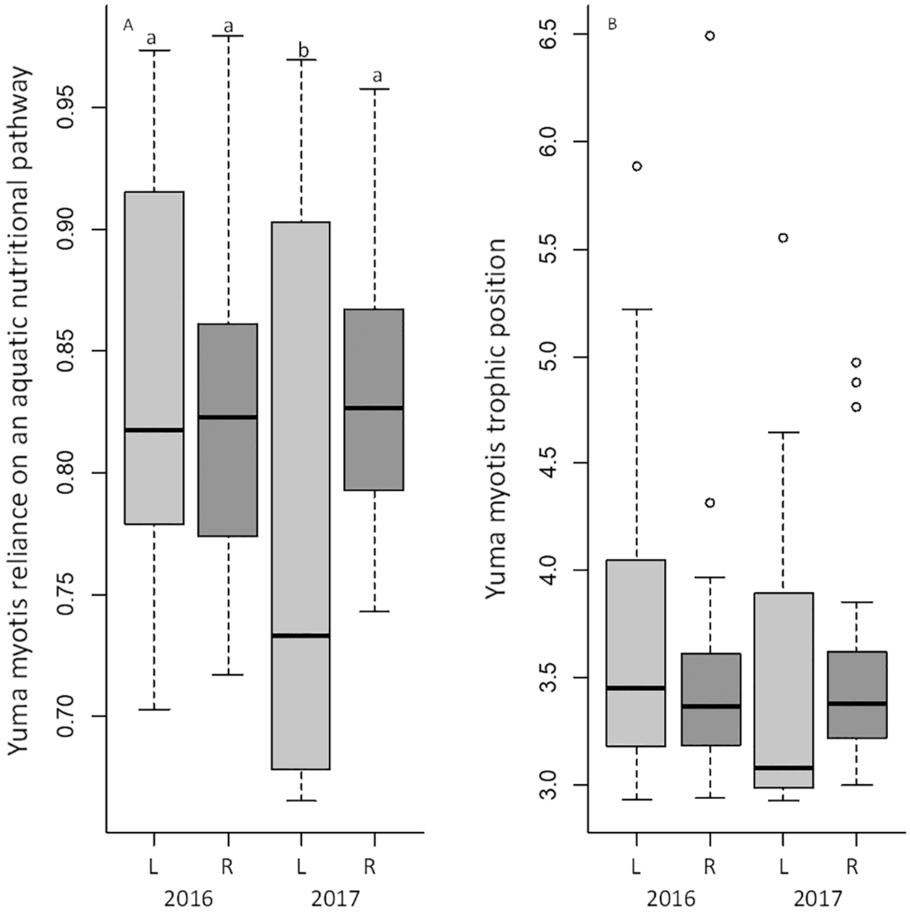

Fig. 3. Box-and-whisker plots depicting (A) reliance on an aquatic nutritional pathway by and (B) trophic position of Yuma myotis compared by site and year. Sites are represented as (L) lower unregulated and (R) regulated. The black lines represent the median of each variable, boxes represent the first and third quartiles, whiskers represent the minimum and maximum values, and open circles represent outliers. Significant differences are indicated by lower-case letters. See Appendix S1: Table S5 for full ANOVA.

2017 may have had both direct and indirect impacts to emergent aquatic insects. Benthic insect abundance and therefore emergence may have been suppressed by direct mortality and displacement caused by scouring floods. Furthermore, algal biomass in both systems was lower in 2017 compared to 2016 due to scouring flows (J. G. Holmquist, *personal communication*). This may have resulted in cascading effects whereby benthic insects that consume algae either were less productive and made up a smaller proportion of available prey to birds and bats, or that benthic insects relied more strongly on allochthonous inputs of organic matter regardless of their feeding preference. However, this does not explain why the effect in bats was only realized at the unregulated site.

Bats relied more strongly on an aquatic nutritional pathway in 2016 compared to 2017, and this difference was largely driven by changes at the unregulated site. In comparison, we saw no change in reliance on an aquatic nutritional pathway at the regulated site between years, and variation in both metrics was greater across years at the unregulated site (Fig. 3, Appendix S1: Table S5). The regulated site is typically characterized by higher algal biomass and dominance of chironomid taxa in the benthic invertebrate community (J. G. Holmquist, *unpublished data*) presumably driven by relatively warm winter water temperature and decreased discharge. In 2017, scouring flows decreased algal biomass and dominance of Chironomidae in both the regulated and unregulated system compared to 2016. However, both metrics remained significantly higher in the regulated river system compared to the unregulated system. Yuma myotis consume chironomids (Brigham et al. 1992), which may in part explain why bats showed consistent reliance on an aquatic nutritional pathway at the regulated site in both the wet and dry year.

We expected to observe greater reliance on an aquatic nutritional pathway by birds breeding in the unregulated river system because of increased access to aquatic prey. Subsidies may be muted if recipient consumers have generalist feeding preferences (Uesugi and Murakami 2007, Royan et al. 2013) and/or lack the mobility to take advantage of localized insect emergence. This may be particularly important for breeding birds compared to bats because some birds, such as black-headed grosbeaks and song sparrows, consume both plant material and insects and generally remain within their territories to minimize time away from nests (Arcese and Smith 1988, Martin et al. 2000). For example, yellow warblers prey on emergent aquatic insects in proportion to their relative abundance rather than exhibiting exclusive preference (Busby and Sealy 1979). Opportunistic consumption of abundant insect taxa even contributes to convergence in prey choice despite differences in species' foraging strategies and morphology (Rotenberry 1980, Rosenberg et al. 1982, Trevelline et al. 2018). Birds sampled in this study derived greater than 50% of their energetic needs on average from aquatic food webs during our sampling period, irrespective of river regulation. This suggests that emergent aquatic insect abundance in both systems must be high enough that birds exploit the subsidy despite generalist feeding preferences and limited mobility compared to bats.

We acknowledge that $\delta^{13}C$ values for algae can vary greatly by season (Finlay 2004), and we collected algae in mid-summer to represent the height of the growing season and also because river access was safer. This may have led to asynchrony with the timing of tissue collection from birds (as they were sampled in May and June) and therefore potential uncertainty in our estimate of reliance on an aquatic nutritional pathway.

Several studies have examined the relationship between floods and food chain length, with results indicating a positive effect (Sullivan et al. 2015, Jackson and Sullivan 2018), negative effect (Parker and Huryn 2006, McHugh et al. 2010, Sabo et al. 2010), or no effect (Thompson and Townsend 1999). Working in the same study area, Jackson and Sullivan (2018) found that higher magnitude predictable floods were associated with longer food chains leading to tetragnathid spiders. Because regulated rivers tend to have dampened hydrographs relative to unregulated systems, we predicted that trophic position of riparian consumers would be lower in the regulated river system. However, we found no difference in trophic position of bats between systems, and although we did not compare trophic position of bird species between study sites, we did compare $\delta^{15}N$ in bird blood between sites and found only one significant difference. Song sparrow blood was significantly more enriched in ^{15}N at the regulated site compared to the unregulated upper site (Appendix S1: Table S5, Fig. S2), potentially indicating that song sparrows are feeding at a higher trophic position at the regulated study site, although we cannot rule out basal resource heterogeneity in $\delta^{5}N$ as the underlying cause (Cabana and Rasmussen 1996).

Trophic position of bats did not vary between years; however, blood collected from black-headed grosbeaks had significantly higher $\delta^{15}N$ values in 2016 compared to 2017 at both study locations (Appendix S1: Table S5, Fig. S2), potentially indicating that black-headed grosbeaks were feeding at a higher trophic position in 2016. Black-headed grosbeaks are omnivores, and they eat both plant material and invertebrates (Ortega and Hill 2010). Therefore, a higher trophic position may simply indicate increased reliance on invertebrate prey, whether aquatic or terrestrial in origin.

Hetch Hetchy Reservoir managers attempt to mimic seasonal floods on the Tuolumne River downstream of the reservoir to promote intact ecosystem processes. Managers plan water releases to mobilize bed sediments, prevent encroachment of riparian shrubs along river banks and channel bars (e.g., Bendix and Hupp

2000, Miller et al. 2013), and to inundate floodplain wetlands in Poopenaut Valley. For example, in 2016, a simulated flood successfully mobilized bed sediments and reduced willow cover, which may have enhanced distribution of riparian invertebrate prey (Greenwood 2014) and foraging capabilities of bats (Hagen and Sabo 2012). Wetland inundation is also associated with increased abundance and diversity of both terrestrial and aquatic invertebrates (Holmquist and Schmidt-Gengenbach 2019), and promotes the growth of wetland plants, which in turn provide cover for breeding birds and ready access to insect prey (van Oort et al. 2015). Our results suggest that current reservoir management practices that include managed scouring floods and floodplain inundation in at least some years may be sufficient to support aquatic–terrestrial food webs leading to birds and bats, with an effect comparable to the unregulated river. However, more work is needed to understand the interaction between interannual differences in precipitation regimes and river regulation for influencing food web attributes.

Comparison with other studies

While other researchers have used stable isotopes to describe diet partitioning of bats (Painter et al. 2009, Lam et al. 2013, and Broders et al. 2014), our study is one of the first to use stable isotopes to describe the importance of aquatic nutritional pathways to bats. Bats drink from water bodies and use riparian corridors for travel (Seidman and Zabel 2001); therefore, observing bats near water does not necessarily imply they are foraging for emergent aquatic insects. Although Yuma myotis are generally assumed to forage primarily on small aquatic insects (Ober and Hayes 2008), our study provides direct evidence that Yuma myotis and other bats in this study area are highly reliant on trophic networks originating with primary production by algae. We estimated that bats captured across our study area relied on an aquatic nutritional pathway for 61–82% of their energetic demand on average by species, and some individuals derived as much as 98% of their carbon from an aquatic nutritional pathway (Table 1). Jackson and Sullivan (2015, 2018) found that tetragnathid spiders in the same study system relied on an aquatic nutritional pathway for 20–90% of their nutritional needs, and Collier et al. (2002) observed that riparian spiders derived 58% of their nutrition from instream sources in a New Zealand stream, and tetragnathid spiders and tree swallows sampled along a mid-order river in Ohio relied on an aquatic nutritional pathway for 34–67% and 14–93% of their nutritional needs, respectively (Kautza and Sullivan 2016, Sullivan et al. 2018). In comparison, the bats sampled in this study were more reliant on an aquatic nutritional pathway than many previously sampled riparian consumers. We acknowledge that by using a single TDF for all taxa and tissues we may be slightly overestimating reliance on an aquatic nutritional pathway, particularly in the case of higher trophic position bats (Ben-David and Flaherty 2012).

Whereas floods deliver organic material, sediments, and nutrients into floodplains (Schindler and Smits 2017), and emergent aquatic insects transport carbon and nutrients farther into the riparian zone (Jonsson et al. 2012, Muehlbauer et al. 2014), our results show that highly mobile species such as birds and bats could transport the energy generated by aquatic production even farther than these previous studies have considered. Thus, the spatial envelope of aquatic–terrestrial ecosystems (e.g., Gurnell et al. 2016) may be much larger than previously estimated by examining less-mobile riparian consumers, underscoring the potential importance of river food webs to organisms and ecosystems typically characterized as terrestrial.

Reliance on aquatic primary production by and trophic position of bats as estimated from hair samples was generally higher than from blood samples, and these patterns were consistent across individuals (Appendix S1: Table S6, Fig. S3). We interpret this to indicate that bats relied more heavily on an aquatic nutritional pathway and fed at a higher trophic position earlier in the summer (most bats were captured in September). Yuma myotis showed considerable individual variability in diet as indicated by trophic position, yet individuals exhibited consistent dietary trends as evidenced by corresponding blood and hair samples (Appendix S1: Table S6, Fig. S3).

For birds, we found few significant relationships between stable isotope signatures of paired blood and feather samples (Appendix S1:

Table S6, Fig. S4), indicating that birds in this study area have flexible feeding preferences throughout the year. This is expected, since many of the bird species sampled are migratory, and may replace their feathers in a different geographic location than Yosemite National Park, where dominant food resources likely differ. For example, black-headed grosbeaks that breed in Yosemite undergo molt-migration, replacing their feathers in Sonora Mexico (Siegel et al. 2016), while warbling vireos may complete part of their annual pre-basic molt on wintering grounds (Pyle 1997). Even resident species such as song sparrow may exhibit flexibility in their feeding preferences, as the feathers we sampled are replaced in the late summer when aquatic prey subsidies are likely diminishing relative to terrestrial sources (Pyle 1997, Nakano and Murakami 2001).

Trophic position of birds in this study ranged from 2.17 to 4.16 on average by species and trophic position of bats ranged from 2.75 to 3.59 on average by species (Table 2). These findings are comparable with other studies that measured food chain length of aquatic–terrestrial systems and used a 3.4‰ per trophic level ^{15}N enrichment factor. For example, Sullivan et al. (2015) reported a range in food chain length from 2.6 to 4.4 which included aquatic and riparian insects, fish, and insectivorous and piscivorous birds. Jackson and Sullivan (2015, 2018) found that tetragnathid spiders in the same study system occupied a trophic position between 1.75 and 3.99, which is comparable with the trophic position of tetragnathid spiders collected from the Scioto River system in Ohio (2.35–3.98, Tagwireyi and Sullivan 2016), and in our study (2.24–3.23, Table 2). Trophic position of birds and bats in this study was also comparable to food chain length estimates of purely aquatic systems (i.e., 2.6–4.2: McHugh et al. 2010), providing additional evidence that riparian insectivores occupy a trophic role similar to predatory fish (Warfe et al. 2013, Sullivan et al. 2015).

Our findings contribute to a growing body of literature linking aquatic processes to terrestrial food webs and suggest that managers consider aspects of ecosystem function and processes that cross ecosystem boundaries when assessing anthropogenic impacts to ecosystems and designing management approaches in regulated rivers.

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LITERATURE CITED

Allen, D. C., K. E. McCluney, S. R. Elser, and J. L. Sabo. 2014. Water as trophic currency in dryland food webs. Frontiers in Ecology and the Environment 12:156–160.

Arcese, P., and J. N. Smith. 1988. Effects of population density and supplemental food on reproduction in song sparrows. Journal of Animal Ecology 57:119–136.

Bartrons, M., M. Papes, M. W. Diebel, C. Gratton, and M. J. Vander Zanden. 2013. Regional-level inputs of emergent aquatic insects from water to land. Ecosystems 16:1353–1363.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201–220.

Bellmoore, J. R., J. R. Benjamin, M. Newsom, J. A. Bountry, and D. Dombroski. 2017. Incorporating food web dynamics into ecological restoration: a modeling approach for river ecosystems. Ecological Applications 27:814–832.

Ben-David, M., and E. A. Flaherty. 2012. Stable isotopes in mammalian research: a beginner's guide. Journal of Mammology 93:312–328.

Bendix, J., and C. R. Hupp. 2000. Hydrologic and geomorphological impacts on riparian plant communities. Hydrological Processes 14:2977–2990.

Brigham, R. M., H. D. J. N. Aldridge, and R. L. Mackey. 1992. Variation in habitat use and prey selection by Yuma bats, *Myotis yumanensis*. Journal of Mammalogy 73:640–645.

Broders, H. G., L. J. Farrow, R. N. Hearn, L. M. Lawrence, and G. J. Forbes. 2014. Stable isotopes reveal that little brown bats have a broader dietary niche than northern long-eared bats. BioOne 16:315–325.

Bugoni, L., R. A. R. McGill, and R. W. Furness. 2008. Effects of preservation methods on stable isotope signatures in bird tissues. Rapid Communication in Mass Spectrometry 22:2457–2462.

Busby, D. G., and S. G. Sealy. 1979. Feeding ecology of a population of nesting yellow warblers. Canadian Journal of Zoology 57:1670–1681.

Cabana, G., and J. B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences USA 93:10844–10847.

Carey, C. 2009. The impacts of climate change on the annual cycles of birds. Philosophical Transactions of the Royal Society B 364:3321–3330.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors (^{15}N and ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453.

Chen, W., and J. D. Olden. 2017. Designing flows to resolve human and environmental water needs in a dam-regulated river. Nature Communications 8:2158.

Collier, K., S. Bury, and M. Gibbs. 2002. A stable isotope study of linkages between stream and terrestrial food webs through spider predation. Freshwater Biology 47:1651–1659.

Crawley, M. J. 2007. The R Book. First edition. John Wiley & Sons, Chichester, UK.

DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochima Acta 42:495–506.

Dettinger, M. D., F. M. Ralph, T. Das, P. J. Neiman, and D. R. Cayan. 2011. Atmospheric rivers, floods and the water resources of California. Water 3:445–478.

Downing, A. L., and M. A. Leibold. 2010. Species richness facilitates ecosystem resilience in aquatic food webs. Freshwater Biology 55:2123–2137.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science 266:753–762.

Finlay, J. C. 2001. Stable-carbon-isotope ratios of river biota: implications for energy flow in lotic food webs. Ecology 82:1052–1064.

Finlay, J. C. 2004. Patterns and controls of lotic algal stable carbon isotope ratios. Limnology and Oceanography 49:850–861.

Frick, W. F., J. R. Shipley, J. F. Kelly, P. A. Heady III, and K. M. Kay. 2014. Seasonal reliance on nectar by an insectivorous bat revealed by stable isotopes. Oecologia 174:55–65.

Gratton, C. J., and M. J. Vander Zanden. 2009. Flux of aquatic insect productivity to land: comparisons of lentic and lotic ecosystems. Ecology 90:2689–2699.

Greenwood, M. J. 2014. More than a barrier: the complex effects of ecotone vegetation type on terrestrial consumer consumption of an aquatic prey resource. Austral Ecology 39:941–951.

Gurnell, A. M., W. Bertoldi, K. Tockner, G. Wharton, and G. Zolezzi. 2016. How large is a river? Conceptualizing river landscape signatures and envelopes in four dimensions. WIREs Water 3:313–325.

Hagen, E. M., and J. L. Sabo. 2012. Influence of river drying and insect availability on bat activity along the San Pedro River, Arizona (USA). Journal of Arid Environments 84:1–8.

Hicks, B. J., M. S. Wipfli, D. W. Lang, and M. E. Lang. 2005. Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, southcentral Alaska. Oecologia 144:558–569.

Holmquist, J. G., and J. Schmidt-Gengenbach. 2019. Arthropod assemblages in a montane wetland complex: influences of adjoining lotic and lentic habitat and temporal variability. Wetlands 40:259–271.

Jackson, B. K., and S. M. P. Sullivan. 2015. Responses of riparian tetragnathid spiders to wildfire in forested ecosystems of the California Mediterranean climate region, USA. Freshwater Science 34:1542–1557.

Jackson, B. K., and S. M. P. Sullivan. 2018. Ecosystem size and flooding drive trophic dynamics of riparian spiders in a fire-prone Sierra Nevada river system. Canadian Journal of Fisheries and Aquatic Sciences 75:308–318.

Jonsson, M., P. Deleu, and B. Malmqvist. 2013. Persisting effects of river regulation on emergent aquatic insects and terrestrial invertebrates in upland forests. River Research and Applications 29:537–547.

Jonsson, M., D. Strasevicius, and B. Malmquist. 2012. Influences of river regulation and environmental variables on upland bird assemblages in northern Sweden. Ecological Research 27:945–954.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Pages 110–127 *in* Dodge, D. P. editor. Proceedings of the International Large River Symposium (LARS). Canadian Journal of Fisheries and Aquatic Sciences Special Publication 106, NRC Research Press, Ottawa, Ontario, Canada.

Kautza, A., and S. M. P. Sullivan. 2016. The energetic contributions of aquatic primary producers to terrestrial food webs in a mid-size river system. Ecology 97:694–705.

Kennedy, T. A., J. D. Muelbauer, C. B. Yackulic, D. A. Lytle, S. W. Miller, K. L. Dibble, E. W. Kortenhoeven, A. N. Metcalfe, and C. V. Baxter. 2016. Flow management for hydropower extirpates aquatic insects, undermining river food webs. BioScience 66:561–575.

Kunz, T., R. Hodgkison, and C. D. Weise. 2009. Methods of capturing and handling bats. Pages 3–35 *in* T. Kunz and S. Parsons, editors. Ecological and behavioral methods for the study of bats. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Lam, M. M., D. Martin-Creuzburg, K. Rothhaupt, K. Safi, E. Yohannes, and I. Salvarina. 2013. Tracking diet preferences of bats using stable isotope and fatty acid signatures of faeces. PLOS ONE 8:e83452.

Luo, L., D. Apps, S. Arcand, H. Xu, M. Pan, and M. Hoerling. 2017. Contributions of temperature and precipitation anomalies to the California drought during 2012–2015. Geophysical Research Letters 44:3184–3192.

MacCarthy, K. A., T. C. Carter, B. J. Steffen, and G. A. Feldhamer. 2006. Efficacy of the mist-net protocol for Indiana bats: A video analysis. Northeastern Naturalist 13:25–28.

Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects on resource subsidies. Ecology 88:140–148.

Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity; separating nest site and parental activity effects. Proceedings of the Royal Society B 267:2287–2293.

Martinez del Rio, C. M., N. Wolf, S. A. Carleton, and L. Z. Gannes. 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biological Review 84:91–111.

McBain and Trush, Inc. 2007. Upper Tuolumne River: description of river ecosystem and recommended monitoring actions. Prepared for the San Francisco Public Utilities Commission Land and Natural Resources Division, San Francisco, California, USA.

McHugh, P. A., A. R. McIntosh, and P. G. Jellyman. 2010. Dual influences of ecosystem size and disturbance on food chain length in streams. Ecology Letters 13:881–890.

Miller, K. A., J. A. Webb, S. C. de Little, and M. J. Stewardson. 2013. Environmental flows can reduce the encroachment of terrestrial vegetation into river channels: a systematic literature review. Environmental Management 52:1202–1212.

Muehlbauer, J. D., S. F. Collins, M. W. Doyle, and K. Tockner. 2014. How wide is a stream? Spatial extent of potential "stream signature" in terrestrial food webs using meta-analysis. Ecology 95:44–55.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial–aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435–2441.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences USA 98:166–170.

Nilson, C., C. A. Reidy, M. Dynesius, and C. Ravenga. 2005. Fragmentation and flow regulation of the world's large river systems. Science 308:405–408.

Ober, H. K., and J. P. Hayes. 2008. Prey selection by bats in forests of western Oregon. Journal of Mammalogy 89:1191–1200.

Ortega, C., and G. E. Hill. 2010. Black-headed Grosbeak (*Pheucticus melanocephalus*). *in* A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Owen, J. C. 2011. Collecting, processing, and storing avian blood: a review. Journal of Field Ornithology 82:339–354.

Painter, M. L., C. L. Chambers, M. Siders, R. R. Doucett, J. O. Whitaker, and D. L. Phillips. 2009. Diet of spotted bats (*Euderma maculatum*) in Arizona as indicated by fecal analysis and stable isotopes. Canadian Journal of Zoology 87:865–875.

Palmer, M. A., and C. M. Febria. 2012. The heartbeat of ecosystems. Science 336:1393–1394.

Parker, S. M., and A. D. Huryn. 2006. Food web structure and function in two Arctic streams with contrasting disturbance regimes. Freshwater Biology 51:1249–1263.

Parnell, A., and R. Inger. 2019. Stable isotope mixing models in R. Available at https://cran.r-project.org/web/packages/simmr/vignettes/simmr.html

Parsons, S., and J. M. Szewczak. 2009. Detecting, recording and analyzing the vocalizations of bats. Pages 91–111 *in* T. Kunz and S. Parsons, editors. Ecological and behavioral methods for the study of bats. Johns Hopkins University Press, Baltimore, Maryland, USA.

Pearson, S. F., D. J. Levey, C. H. Greenberg, and C. Martinez del Rio. 2003. Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. Oecologia 135:516–523.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature 307:321–326.

Pimm, S. L., and J. H. Lawton. 1977. Number of trophic levels in ecological communities. Nature 268:329–331.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47:769–784.

Poff, N. L., and J. D. Olden. 2017. Can dams be designed for sustainability? Science 358:1252–1253.

Poff, N. L., and J. K. H. Zimmerman 2010. Ecological responses to altered flow regimes: a literature review to inform environmental flows science and management. Freshwater Science 55:194–205.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Power, M. E. 1992. Hydrologic and trophic controls of seasonal algal blooms in northern California rivers. Archivs fiir Hydrobiologie 125:385–410.

Power, M. E. 1995. Floods, food chains and ecosystem processes in rivers. Pages 52–60 *in* C. Jones and J. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.

Power, M. E., M. S. Parker, and J. T. Wootton. 1995. Disturbance and food chain length in rivers. Pages 286–297 *in* G. Polisand K. Winemiller, editor. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Pyle, P. 1997. Identification guide to North American birds, part I. Slate Creek Press, Bolinas, California, USA.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. USDA Forest Service, Albany, California, USA.

Rosenberg, K. V., R. D. Ohmart, and B. W. Anderson. 1982. Community organization of riparian breeding birds: response to an annual resource peak. The Auk 99:260–274.

Rotenberry, J. T. 1980. Dietary relationships among shrub steppe passerine birds: competition or opportunism in a variable environment? Ecological Monographs 50:93–110.

Royan, A., D. M. Hannah, S. J. Reynolds, D. G. Noble, and J. P. Sadler. 2013. Avian community responses to variability in river hydrology. PLOS ONE 8: e83221.

Russo, T. A., A. T. Fisher, and J. W. Roche. 2011. Improving riparian wetland conditions based on infiltration and drainage behavior during and after controlled flooding. Journal of Hydrology 432–433:98–111.

Sabo, J. L., J. C. Finlay, T. Kennedy, and D. M. Post. 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. Science 330:965–967.

Sabo, J. L., J. C. Finlay, and D. M. Post. 2009. Food chains in freshwaters. Annals of the New York Academy of Sciences 1162:187–220.

Schindler, D. E., and A. P. Smits. 2017. Subsidies of aquatic resources in terrestrial ecosystems. Ecosystems 20:78–93.

Seidman, V. M., and C. J. Zabel. 2001. Bat activity along intermittent streams in northwestern California. Journal of Mammalogy 82:738–747.

Siegel, R. B., R. Taylor, J. F. Saracco, L. Helton, and S. Stock. 2016. GPS-tracking reveals non-breeding locations an apparent molt migration of a Black-headed Grosbeak. Journal of Field Ornithology 87:196–203.

Siemers, B. M., S. Greif, I. Borissov, S. L. Voigt-Heucke, and C. C. Voigt. 2011. Divergent trophic levels in two cryptic sibling bat species. Oecologia 166:69–78.

Sikes, R. S. and Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Sullivan, S. M. P., K. Hossler, and C. M. Cianfrani. 2015. Ecosystem structure emerges as a strong determinant of food-chain length in linked stream–riparian ecosystems. Ecosystems 18:1356–1372.

Sullivan, S. M. P., D. W. P. Manning, and R. P. Davis. 2018. Do the ecological impacts of dam removal extend across the aquatic–terrestrial boundary? Ecosphere 9:1–19.

Tagwireyi, P., and S. M. P. Sullivan. 2016. Distribution and trophic dynamics of riparian tetragnathid spiders in a large river system. Marine and Freshwater Research 67:309–318.

Takimoto, G., and D. M. Post. 2013. Environmental determinants of food chain length: a meta-analysis. Ecology Research 28:675–681.

Thomas, S. M., and T. W. Crowther. 2015. Predicting rates of isotopic turnover across the animal kingdom: a synthesis of existing data. Journal of Animal Ecology 84:861–870.

Thompson, R. M., and C. R. Townsend. 1999. The effect of seasonal variation on the community structure and food-web attributes of two streams: implications for food-web science. Oikos 87:75–88.

Trevelline, B. K., T. Nuttle, B. D. Hoenig, N. L. Brouwer, B. A. Porter, and S. C. Latta. 2018. DNA metabarcoding of nestling feces reveals provisioning of aquatic prey and resource partitioning among neotropical migratory songbirds in a riparian habitat. Oecologia 187:85–98.

Uesugi, A., and M. Murakami. 2007. Do seasonally fluctuating aquatic subsidies influence the distribution pattern of birds between riparian and upland forests? Ecological Research 22:274–281.

USFWS (United States Fish and Wildlife Service). 2016. Revised Decontamination Protocol. Available online from www.whitenosesyndrome.org/topics/decontamination

USGS (United States Geological Survey). 2018. Surface Water data for California: USGS Surface-Water Annual Statistics. https://waterdata.usgs.gov/ca/nwis/annual

van Oort, H., D. J. Green, M. Hepp, and J. M. Cooper. 2015. Do fluctuating water levels alter nest survivorship in reservoir shrubs? Condor 117:376–385.

Vander Zanden, M. J., M. K. Clayton, E. K. Moody, C. T. Solomon, and B. C. Weidel. 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLOS ONE 10:e0116182.

Vanderklift, M. A., and S. Ponsard. 2003. Sources of variation in consumer-diet ^{15}N enrichment: a meta-analysis. Oecologia 136:169–182.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Waddle, T. J., and J. G. Holmquist. 2013. Macroinvertebrate response to flow changes in a subalpine stream: predictions from two-dimensional hydrodynamic models. River Research and Application 29:366–379.

Warfe, D. M., T. D. Jardine, N. E. Pettit, S. K. Hamilton, B. J. Pusey, S. E. Bunn, and P. M. Davies. 2013. Productivity, disturbance and ecosystem size have no influence on food chain length in seasonally connected rivers. PLOS ONE 8:e66240.

Weller, T. J., S. A. Scott, T. J. Rodhouse, P. C. Ormsbee, and J. M. Zinck. 2007. Field identification of the cryptic vespertilionid bats, *Myotis lucifugus* and *M. yumanensis*. Acta Chiropterologica 9:133–147.

Wimsatt, J., T. J. O'Shea, L. E. Ellison, R. D. Pearce, and V. R. Price. 2005. Impacts of anesthesia and blood sampling on bat survival. Journal of Wildlife Diseases 41:87–95.

Wootton, K. L., and D. B. Stouffer. 2016. Species traits and food-web complexity interactively affect a food web's response to press disturbance. Ecosphere 7:e01518.

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