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RESEARCH ARTICLE

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Insectivorous bat foraging tracks the availability of aquatic flies (Diptera)

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Abstract

Rivers and their adjacent riparian zones are model ecosystems for observing cross-ecosystem energy transfers. Aquatic insects emerging from streams, for example, are resource subsidies that support riparian consumers such as birds, spiders, lizards, and bats. We collaborated with recreational river runners in Grand Canyon, Arizona, USA, to record acoustic bat activity and sample riparian insects using light traps at dusk from April through October 2017–2020. River runners collected these data on 1,428 events over 611 sampling nights at 410 sites throughout a 470-km segment of the Colorado River. We documented 71 insect taxa in light traps and recorded 19 bat species with acoustic detectors. We hypothesized that bat activity along this highly regulated river segment would be influenced primarily by variation in prey availability, as compared to other habitat descriptors. We predicted that bat activity would be positively related to aquatic insect catch rates and unrelated to terrestrial insect abundance. We fit Bayesian regression models to test these hypotheses and to quantify the relationship between bat activity and a suite of environmental variables: time of year, time of day, distance from perennial tributaries, distance from rapids, channel width, geomorphic

reach, tall vegetation cover, air temperature, and lunar phase. Bat activity was positively related to the abundance of aquatic flies (Diptera), which outcompeted all other prey categories and structural habitat descriptors in our models. Within our dusk sampling period, activity of small myotis (California myotis [*Myotis californicus*] and Yuma myotis [*M. yumanensis*]) was high late in the evening and canyon bats (*Parastrellus hesperus*), conversely, were more active early in the evening. Activity of canyon bats varied seasonally, with peak activity in August. Our results support the hypothesis that aquatic prey, specifically aquatic flies, are key predictors of bat activity along a large, regulated river corridor and demonstrate the power of community science as a tool for ecosystem monitoring.

KEYWORDS

aquatic insects, aquatic-terrestrial linkages, bat foraging, Bayesian modeling, citizen science, Colorado River, community science, Glen Canyon Dam, remote sensing, river regulation

Energy transfers across adjacent ecosystems can represent an important energetic subsidy for the recipient ecosystem, but these subsidies are rarely considered in research study designs (Polis et al. 1997). Rivers and their riparian zones are model ecosystems for quantifying the role of cross-ecosystem energy transfer (Baxter et al. 2005, Muehlbauer et al. 2014). Riparian ecosystems deliver nutrients and organic matter such as fallen vegetation and terrestrial insects to rivers. In the opposite direction, rivers can fuel food webs in riparian zones via emergence of adult aquatic insects (Power and Rainey 2000, Baxter et al. 2005). Aquatic insects emerging from streams are important energetic subsidies that support riparian consumers such as birds (Nakano and Murakami 2001), spiders (Kato et al. 2003), lizards (Sabo and Power 2002), and bats (de Jong and Ahlén 1991, Fukui et al. 2006, Hagen and Sabo 2011).

Bats are common along rivers because of prey availability (Jackson et al. 2020), the structure of riparian vegetation (Hagen and Sabo 2011), and the many other ecosystem services that rivers provide (Graziano et al. 2022). Owing to habitat degradation, climate-induced drought, and the spread of white nose syndrome, 15% of bat species are threatened by extinction and numerous species are threatened or of conservation concern (Frick et al. 2020, Cheng et al. 2021). Preserving aquatic resources is an important consideration in sustaining bat populations (Rogers et al. 2006, Korine et al. 2016, Russo et al. 2016).

Approximately 70% of bats worldwide are insectivores (Ammerman et al. 2012). Foraging activity by insectivorous bats varies with species, sex, reproductive stage, echolocation strategy, habitat, season, predation, competition, and prey availability (Adams 2003, Gordon et al. 2019). Foraging itself is an energy-intensive activity that requires high caloric expenditure (de Jong and Ahlén 1991). Common prey items for bats are flies, moths, beetles, grasshoppers, flying ants, mayflies, stoneflies, and caddisflies (Clare et al. 2011, Ammerman et al. 2012, Demere 2016), some of which have fully aquatic juvenile life stages. Subsidies of aquatic insects emerging from rivers are particularly important to riparian food webs in ecosystems where terrestrial production is low, such as arid or desert ecosystems (Lupoli et al. 2021).

Aquatic insects are well-documented prey for native and desired non-native fish in the Colorado River in Arizona, USA (Cross et al. 2013, Kennedy et al. 2016, Korman et al. 2021), but few studies have investigated the role of emergent aquatic insects as prey for terrestrial wildlife in Grand Canyon (Yard et al. 2004, Lupoli 2021). Aquatic invertebrate assemblages of the Colorado River in Grand Canyon are simplified and dominated by generalist aquatic

insect taxa, particularly aquatic flies in the family Chironomidae, and non-insects (e.g., crustaceans, snails, mussels, worms), which lack a terrestrial life stage and are therefore largely unavailable to terrestrial wildlife. Unstable food webs and reduced biodiversity are prevalent in regulated rivers (Power et al. 1996, Abernethy et al. 2021), especially below dams with hydropeaking practices (Bätz et al. 2022) such as Glen Canyon Dam.

We collaborated with recreational river runners and other community scientists from 2017–2020 to simultaneously sample acoustic bat activity and emergent insects along a 470-km segment of the highly regulated Colorado River downstream of Glen Canyon Dam. We hypothesized that bat activity along this highly regulated river segment is influenced primarily by variation in prey availability, as compared to other habitat components. We predicted that bat activity would be positively related to aquatic insect abundance and that prey availability would outcompete other environmental variables as a predictor of bat activity. Additionally, we predicted that terrestrial insect abundance would be low compared to aquatic insect abundance, and in turn bat activity along the river corridor would be unrelated to terrestrial insects.

STUDY AREA

We sampled along the shorelines of a 470-km segment of the Colorado River in Grand Canyon National Park and Glen Canyon National Recreation Area, Arizona between April and October in 2017–2020. Our sampling extended from 6 km downstream of Glen Canyon Dam near Page, Arizona (Lees Ferry; elevation of 945 m) to Pearce Ferry near the upper boundary of Lake Mead (elevation of 367 m; Figure 1). The Colorado River in Grand Canyon is characterized by stretches of relatively flat water punctuated by large, steep rapids that generally arise from debris flows at tributaries. Discharge of the river is primarily determined by releases from Glen Canyon Dam, a 216-m-tall hydropower dam that forms Lake Powell. The Colorado River basin supplies municipal water to nearly 40 million people. Grand Canyon sits between Lake Powell and Lake Mead, which are the 2 largest reservoirs by volume in the

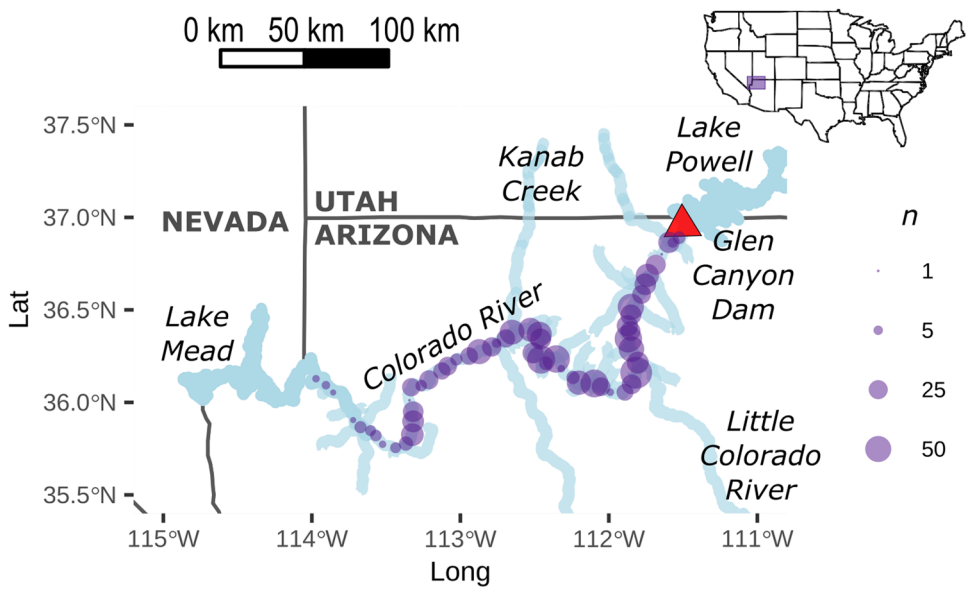

FIGURE 1 Sampling locations for bat and insect data collection from 2017–2020 along the Colorado River in Grand Canyon, Arizona, USA, binned in 8-km river segments for visibility. The size of the circles represents the number of individual samples (*n*) in each river segment. The red triangle shows the location of Glen Canyon Dam. Lat = latitude. Long = longitude.

United States. The river corridor in Grand Canyon is protected as a wilderness area by the National Park Service and is a popular backcountry recreation destination with visitation managed through a permitting system. The river channel averages 70 m in width at a discharge of 227 m^3/second, though it ranges from 22–407 m in width along our study area (Magirl et al. 2008). Air temperatures during our study period ranged from 12.5–41.7°C. The Grand Canyon region is an arid desert with little precipitation (<25 cm/yr) though summers are characterized by intense and short conductive storms (i.e., monsoons). Our sampling took place within 9 m of the water's edge in the riparian zone at recreational campsites characterized by sand beaches vegetated with coyote willow (*Salix exigua*), baccharis (*Baccharis salicifolia*, *B. sarothroides*, and *B. salacina*), arrowweed (*Pluchea sericea*), and tamarisk (*Tamarix* spp.). Common bat species along the river corridor are canyon bats (*Parastrellus hesperus*), California myotis (*Myotis californicus*), Yuma myotis (*M. yumanensis*), and Mexican free-tailed bats (*Tadarida brasiliensis*).

METHODS

Bat acoustic sampling

We used Echometer Touch detectors (first edition, Wildlife Acoustics, Maynard, MA, USA) paired with handheld tablets (iPad mini 4, software version 13.3.1, Apple, Cupertino, CA, USA) to record bats. We chose the Echometer because it was a commercially available full-spectrum acoustic detector that also allows real-time visualization and interpretation of bat activity. Because the community collected these data, education and outreach value were important considerations in methods design (Metcalfe et al. 2022). Participants in this project included commercial river guides, private river runners, and academic trips through universities and high school groups via our involvement in the Partners in Science program with Grand Canyon Youth. We trained community scientists to use this equipment before their expeditions in addition to providing a written protocol. On each night of their trip, community scientists initiated bat recordings within 1 hour after sunset. Microphones were directed toward the river and deployed adjacent to the river's edge (0–9 m). Community scientists were allowed to move around camp with their tablets for outreach purposes (e.g., sharing the tablet screen with interested trip participants), though most deployments were ultimately stationary and near the river. Sampling duration ranged from 30–90 minutes. We trimmed recording sessions that exceeded this range to 90 minutes and excluded sessions shorter than 30 minutes from analyses.

We initially assigned species to each recording using Kaleidoscope (software version 2.2.9, Wildlife Acoustics; Table S1, available in Supporting Information) and later manually examined these recordings for incongruities. We used the results of the Kaleidoscope auto-identification process to quantify the nightly number of recordings. Kaleidoscope assigned a single species likelihood identification to each recording. We combined recordings assigned to California and Yuma myotis into a single response variable (small myotis) because of overlap in the echolocation call characteristics of these 2 species. Similarly, we combined recordings that were auto-classified as western red bat (*Lasiurus blossevillii*) and canyon bat into a single response variable of canyon bat because similarities between the echolocation characteristics of these species rendered them difficult for Kaleidoscope to distinguish and because we were unable to confirm a single western red bat during manual review (SI Methods, available in Supporting Information).

To verify species presence by month, we sorted recordings auto-identified by Kaleidoscope by month (Apr–Oct) for each species. In instances where Kaleidoscope assigned large numbers of files to a particular species, we used the automated identification module of SonoBat (version 4.4.5, SonoBat, Arcata, CA, USA) to prioritize manual review to those recordings most likely to be confirmed to species. We conducted annual verification of files by viewing spectrograms in Sonobat using the Northern Arizona classifier. Once we visually confirmed species presence for a particular month, we did not continue manual review of recordings for the species.

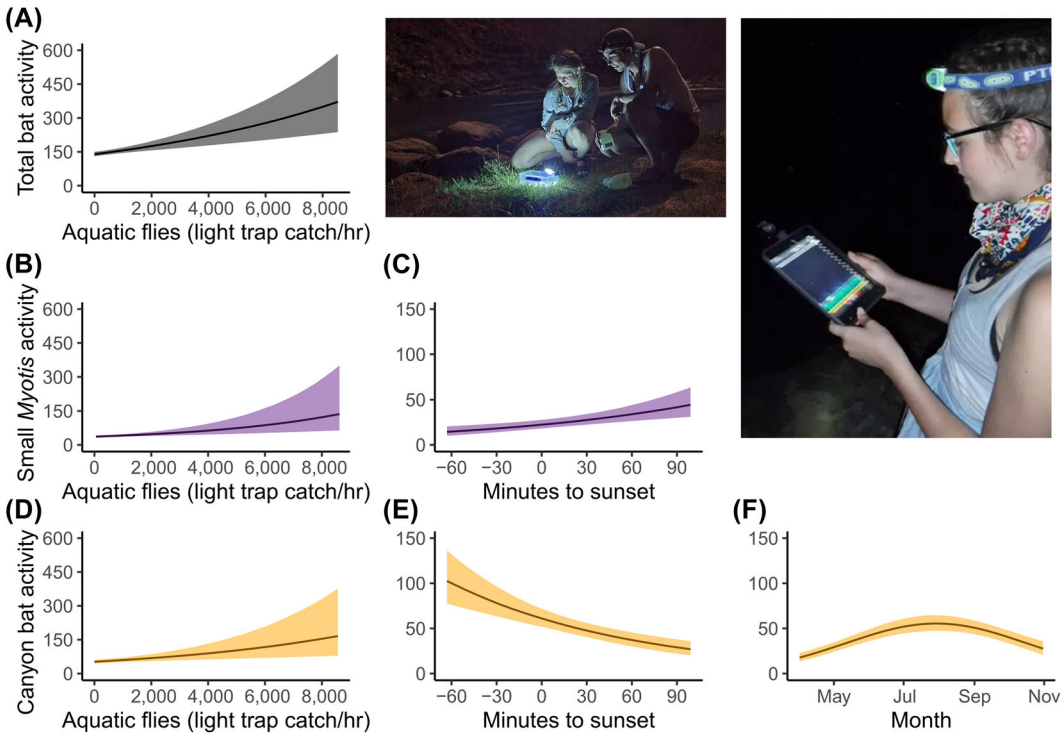

FIGURE 2 We collaborated with community scientists to simultaneously record bat activity using Echometer Touch bat detectors and sample flying insects using light traps (inset photos). Sampling was conducted from 2017–2020 along the Colorado River in Grand Canyon, Arizona, USA. For the most highly supported model in each set representing total bats, Canyon bats, and small *Myotis* species (California and Yuma myotis), we plotted predicted bat activity with standard error across the observed range of each fixed effect (panels A–F). Photos by A. N. Metcalfe (left) and G. M. C. Hopkins (right).

Insect sampling

We sampled aquatic insects using light traps via an established community science monitoring program (Kennedy et al. 2016). Light traps are plastic containers (17 × 28-cm opening and 7 cm deep) filled with 250 mL of ethanol with a battery-operated fluorescent light placed on the short edge of the container (Figure 2A). The lights attract flying insects, which then get trapped and preserved in the ethanol. Community scientists set out light traps within 3 m of the river's edge concurrently with bat detectors (within 1 hour of sunset). After 1 hour, collectors turned off the light trap and transferred the contents to a labeled 250-mL plastic bottle. We processed and archived samples at the United States Geological Survey (USGS) Grand Canyon Monitoring and Research Center, Flagstaff, Arizona. In the lab, we counted and identified insects to family and species as possible. We calculated insect abundance as catch (*n* individuals) per hour and we only included samples in analyses if sampling duration was between 45 and 90 minutes. We tested for variation in prey catch rates among months and across years using one-way analysis of variance (ANOVA; $\alpha = 0.05$). Sampling for insects using light traps and acoustic recording of bats occurred simultaneously, but relative durations varied (Figure S1, available in Supporting Information).

Hypotheses

We considered 8 different categories of invertebrate prey as model covariates to test competing hypotheses on which prey items best predicted bat activity. Prey availability or light trap catch rates represented the number of individual

insects caught per hour in light traps. We also evaluated aquatic prey, defined as insects that have aquatic life stages (e.g., caddisflies, mayflies, and flies in the families Chironomidae and Simuliidae), and terrestrial prey, defined as insects that are terrestrial throughout the entirety of their lifecycles (e.g., most moths, leaf hoppers, beetles, grasshoppers, muscomorph flies). We evaluated 5 categories of taxa that were most common in light traps: aquatic flies (Diptera), caddisflies (Trichoptera), moths (Lepidoptera), all other aquatic prey, and all other terrestrial prey.

We hypothesized that total bat, small myotis, and canyon bat activity over space and time would be primarily predicted by variation in prey availability as compared to other habitat components. Structural habitat features we considered included geomorphic reach, distance to tributaries, river width, distance to rapids, and vegetation cover. To test for the influence of geomorphic reach on bat activity, we included a random effect that allowed bat activity to vary based on the 11 geomorphic reaches that have been identified for this river section (Schmidt and Graf 1990) and 2 additional geomorphic reaches (Glen Canyon upstream of Lees Ferry and Grand Canyon West downstream of Diamond Creek). Geomorphic reaches represent a wide breadth of geologic and structural abiotic conditions, which affect biota (Durning et al. 2021). For distance from tributary, we included the 21 perennial tributaries to the Colorado River and calculated the distance to closest tributary for each sampling site (up or downstream). Perennial tributaries are additional riparian habitat for foraging bats and confluences are often hotspots of biodiversity. We calculated river width of the wetted channel at 227 m^3/second discharge at 2,689 cross-widths from digital elevation maps created from 2002 airborne imagery during which river discharge was maintained at a steady 227 m^3/second (Magirl et al. 2008). River width is representative of channel morphology and confinement by the canyon walls, which can affect bat movement (Hagen and Sabo 2011). Because the sound of turbulent water can reduce foraging activity in bats (Mackey and Barclay 1989), we included distance from rapid in models. Rapids in Grand Canyon are named, and we included all named rapids in our models, regardless of size or whitewater classification. Finally, because riparian vegetation can provide cover and roosting habitat for bats (Hagen and Sabo 2011), we included the cover of trees and tall shrubs along the riparian corridor (tall vegetation cover) as a covariate. We calculated tall vegetation cover by using high-resolution (20-cm pixel) multispectral (visible and near-infrared) fixed wing airborne imagery acquired in May 2013 (Durning et al. 2016; SI Methods).

Finally, we evaluated the role of temporal and environmental covariates including month, season (ordinal day as linear or quadratic), year, sampling start time, moon phase, and air temperature in influencing bat activity. We compiled moon phase data using the R package Lunar (Lazaridis 2014). We downloaded air temperature data for 2017 to 2020 from a single location—the National Oceanic and Atmospheric Administration weather station at Phantom Ranch (165 km downstream of Glen Canyon Dam) and included it in models both on a daily and monthly scale. Average daily temperatures ranged from 12.5–41.6°C and monthly average temperatures ranged from 20.7–32.1°C.

Model fitting and selection

We used a generalized linear mixed modeling approach with a negative binomial distribution to analyze call rates of bats. Our response variable was the count of bat recordings during each sampling event offset by the log of sampling duration (min) to account for varying levels of sampling effort. Our random effects included sampling date (each unique sample month and year combination), site (sampling location as km downstream of Glen Canyon Dam; river runners repeatedly sampled in popular campsites), and individual collector (identity of each community scientist). We fit models to data using the R package brms (Bürkner 2017), which fits Bayesian models via Hamiltonian Monte Carlo and no-u-turn sampler implemented in Stan (Stan Development Team 2021).

We constructed 3 sets of models to investigate the activity of total bats (all species combined), canyon bats, and small myotis (California and Yuma myotis). For model selection, we incorporated a forward stepwise approach and used leave-one-out cross-validation using the R package loo (Vehtari et al. 2017). We first constructed base models with no explanatory variables, besides the random effects and offset that we included in all models. We did not consider single variable models that did not explain more variability than the base model for multi-variable models. For models with >1 variable, we assessed correlation between variables using the Pearson correlation

coefficient and did not include correlated variables ($|r| > 0.8$) in the same model. We scaled and centered all covariates prior to analysis by subtracting the mean and dividing by the standard deviation. Forward stepwise selection proceeded until the leave-one-out information criterion stopped declining with the addition of covariates.

For each model set, we selected the most highly supported model describing bat activity and plotted the predicted relationship with each covariate across the observed range of data (continuous) or for all levels (discrete) while holding the other fixed covariates at their respective means. We also summarized the most highly supported models by providing the coefficient estimates and measures of uncertainty for each of the fixed effects terms. Finally, we investigated the relative spatial and temporal relationships within the random effects of our most highly supported models by calculating pseudo-R^2 values for the model overall and for each covariate (Yackulic et al. 2020).

RESULTS

Over our 4-year study period, 46 community scientists collected data on insects and bats on 1,428 sampling events from 611 unique sampling dates and at 410 unique sampling sites. We recorded and verified 19 bat species (Table 1). Not all bat recordings were identifiable to species (43.4% of recordings were not assigned a species by Kaleidoscope), though all recordings that contained bat calls were included in models of total bat activity. The majority of recordings (89.1%) were identifiable using auto-identification. California myotis, Yuma myotis, and canyon bats were the 3 most common species detected, comprising almost 50.4% of all calls. Bat species richness was greatest in July with 17 species recorded and was lowest in April with 13 species recorded (Table 1). Following manual examination of our calls, all but the pocketed free-tailed bat (*Nyctinomops femorosaccus*) had been previously acoustically recorded or captured in the Grand Canyon ecoregion.

We identified 71 unique insect taxa in light trap samples among 987,417 individual specimens, with a mean catch rate of 657 insects/hour (Table S2, available in Supporting Information). Aquatic insects accounted for 83.0% of individuals captured, though terrestrial prey were present in 97% of samples. Insect abundance was dominated by 2 aquatic taxa that accounted for 80.2% of all individuals: midges (Chironomidae, 40.7%) in the fly order Diptera and microcaddisflies (Hydroptilidae, 39.6%) in the caddisfly order Trichoptera. Moths (Order Lepidoptera) were the most common terrestrial taxa and represented 27.1% of terrestrial individuals (4.7% of the insect count). Using ANOVA, we found statistically significant variation in prey catch rates across months but not across years ($F = 2.17$, $P = 0.04$ and $F = 0.50$, $P = 0.6$, respectively). Across years, light trap catch rates of prey were greatest in July and August.

The models of total bat activity, small myotis activity, and canyon bat activity all included positive and statistically significant (based on 95% CI) relationships with the number of aquatic flies observed in light traps (Figure 2; Table 2). For total bat activity, the number of aquatic flies was the only covariate included in the best model (Table S3, available in Supporting Information). The 95% confidence intervals describing this relationship did not overlap zero, indicating a statistically significant and positive effect of aquatic flies on total bat activity (Table 2; Figure 2).

Time of evening (sampling start time relative to sunset) was an important predictor for small myotis and canyon bats. Small myotis activity increased with time past sunset (Table S4 and S5, available in Supporting Information; Figure 2C) and canyon bats, conversely, were more active closer to sunset (Figure 2E). The median sampling start time was 11 minutes after sunset, with a range of starting 63 minutes before sunset to 99 minutes after sunset. Phenology, modeled as the quadratic of ordinal day, was also an important predictor for canyon bats with activity peaking in August (Figure 2F). Although the abundance of aquatic flies was included in the best model for each of our 3 response variables, analysis of pseudo-R^2 values indicated that the abundance of aquatic flies explained only a modest proportion of variation in bat activity within the spatial and temporal random effects (Table 2). Aquatic flies explained 39% of the variation in activity across space for canyon bats but only 7–8% of variation in activity across space for total bats and small myotis. Similarly, aquatic flies explained 35% of variation in canyon bat activity across time but only 0–1% of temporal variation for total bats and small myotis.

TABLE 1 Bat species list from acoustic sampling conducted from 2017–2020 along the Colorado River in Grand Canyon, Arizona, USA. Bats were recorded with Echometer Touch 1 and identified using auto-ID software in Kaleidoscope. We manually vetted recordings to verify the presence of each species for each month observed. We present the conservation status (consv status) by indicating those listed as a species of concern (SC) by Arizona Game and Fish Department. References to other records in the Grand Canyon ecoregion: 1 = Hoffmeister (1970), 2 = Drost et al. (2000), 3 = Carpenter et al. (2021), 4 = Valdez et al. (2021), 5 = BatAMP (2023), and 6 = NABat (2023).

Scientific name	Common name	Consv status	*n* recordings (auto-ID)	*n* recordings (verified)	Apr	May	Jun	Jul	Aug	Sep	Oct	Previous records
Antrozous pallidus	Pallid bat		136	23	x	x	x	x	x	x	x	1,2,3,4,5,6
Corynorhinus townsendii	Townsend's big-eared bat	SC	11	13	x	x		x	x	x		1,2,3,4,5,6
Eptescius fuscus	Big brown bat		1,005	14	x	x	x	x	x		x	1,2,3,4,5,6
Euderma maculatum	Spotted bat	SC	39	9	x	x		x	x	x	x	2,3,4,5,6
Eumops perotis	Greater bonneted bat	SC	1,073	48	x	x	x	x	x	x	x	2,3,4,5,6
Idionycteris phyllotis	Allen's lappet-browed bat	SC	1	16	x	x	x	x	x	x		2,3,6
Lasiurus blosseveli	Western red bat		13,756	0								3,4,6
Lasiurus cinereus	Hoary bat		1,756	13	x	x	x	x	x	x	x	2,3,4,5,6
Lasionycteris noctivagans	Silver-haired bat		2,591	19	x	x	x	x	x	x	x	1,2,3,4,5,6
Myotis californicus	California myotis		8,428	47	x	x	x	x	x	x	x	1,2,3,4,5,6
Myotis cilolabrum	Western small-footed myotis	SC	595	16		x	x	x	x	x	x	2,3,4,5,6
Myotis evotis	Long-eared myotis	SC	28	3				x				3,5,6
Myotis lucifugus	Little brown bat		21	5				x			x	3,4
Myotis thysanodes	Fringed myotis	SC	41	14		x	x	x	x	x	x	1,2,3,5,6
Myotis volans	Long-legged myotis		25	3			x			x	x	1,3
Myotis yumanensis	Yuma myotis	SC	33,871	27	x	x	x	x	x	x	x	1,2,3,4,5,6
Nyctinomops femorsaccus	Pocketed free-tailed bat		0	37					x	x	x	
Nyctinomops macrotis	Big free-tailed bat	SC	65	109	x	x	x	x	x	x	x	2,3,4,5,6
Parastrellus hesperus	Canyon bat		48,903	125	x	x	x	x	x	x	x	1,2,3,4,5,6
Tadarida brasiliensis	Mexican free-tailed bat		5,282	117	x	x	x	x	x	x	x	1,2,3,4,5,6

TABLE 2 Model coefficient estimates, standard deviation (SD), lower (LCI) and upper (UCI) confidence intervals, and pseudo-R^2 values representing the amount of variation in bat activity over space (distance downstream from Glen Canyon Dam) and time (month combined with year) that can be explained by the most highly supported model in each set representing total bats, canyon bats, and small myotis (California and Yuma myotis). Values corresponding to the first row of each model set represent the intercept or baseline activity. Collector (identity of person recording bats), site (sampling location), and sampling date (a combination of sampling year and month) were included as random effects and all models included an offset for sampling duration. For the random effects terms, the coefficient values represent the standard deviation across the individual levels of the given group. For instance, the collector values quantify the variation across individual community scientists. We calculated pseudo-R^2 values for each covariate in a secondary model. Sampling was conducted along the Colorado River in Grand Canyon, Arizona, USA, 2017–2020.

	Estimate	SD	95% LCI	95% UCI	pseudo-R^2 space	pseudo-R^2 time
Total bats	4.93	0.04	4.86	5.00	0.08	0.00
Aquatic flies	0.06	0.01	0.03	0.09	0.08	0.00
Collector	0.04	0.03	0.00	0.11		
Site	0.12	0.02	0.08	0.16		
Sampling date	0.14	0.03	0.09	0.20		
Small myotis	3.13	0.10	2.93	3.33	0.07	0.01
Start time	0.13	0.03	0.06	0.19	0.05	0.01
Aquatic flies	0.10	0.03	0.04	0.17	0.08	0.06
Collector	0.25	0.06	0.14	0.39		
Site	0.37	0.05	0.28	0.46		
Sampling date	0.35	0.07	0.24	0.50		
Canyon bats	3.95	0.08	3.79	4.11	0.39	0.35
Day + day^2	−0.12	0.08	−0.26	0.03	0.59	0.57
Start time	−0.15	0.03	−0.21	−0.09	0.34	0.09
Aquatic flies	0.08	0.03	0.03	0.13	0.06	0.02
Collector	0.33	0.06	0.22	0.47		
Site	0.06	0.04	0.00	0.14		
Sampling date	0.11	0.05	0.02	0.21		

DISCUSSION

Bat activity

Our hypothesis that bat activity was influenced by aquatic prey availability was supported. Bat activity along the river corridor in Grand Canyon at dusk is greatest when and where there is high availability of aquatic flies. Previous researchers demonstrated that prey availability is an important factor influencing bat activity along river corridors (Fukui et al. 2006, Hagen and Sabo 2011) and our study further supports this link between aquatic prey abundance and bat activity in a highly regulated river (Carothers and Brown 1991, Kennedy et al. 2016). Our results add to the growing evidence demonstrating the importance of aquatic subsidies to terrestrial consumers (Nakano and Murakami 2001, Muehlbauer et al. 2014, Collins et al. 2020).

Lizards, mice, and bats are dietarily linked to river-derived carbon sources in Grand Canyon (Lupoli 2021). Our results suggest that a major source of river-derived carbon for bats in Grand Canyon is aquatic flies in the family Chironomidae, though further dietary analysis is merited. An important caveat is that our study is correlative in nature and does not provide direct evidence of bat feeding being tied to increased aquatic insect abundance. Nonetheless, the positive relationship between bat activity and aquatic flies suggests that these insects are a prey source and that this correlation was not based solely on a shared affinity for the same habitat conditions. Another important caveat is that we did not explicitly consider detection probability in our modeling efforts. Detection of bats and prey can be affected by a suite of variables. For example, to protect our equipment, we did not sample in high wind or rain conditions, which would be low detection probability events.

Models that included aquatic flies outcompeted all other prey categories, including terrestrial moths and other aquatic insects such as caddisflies. Aquatic flies in Grand Canyon are dominated by the family Chironomidae (95% of the aquatic flies we captured in this study were chironomids). Chironomids are common in rivers including in the tailwaters immediately downstream of dams. For example, chironomids were among the dominant insect taxa in a recent study of invertebrate assemblages in 7 different tailwater segments of the Colorado River (Abernethy et al. 2021). Bats downstream of O'Shaughnessy Dam on the Tuolumne River, Yosemite National Park, California, USA, including myotis and canyon bats are associated with the presence of abundant emergent chironomids (Jackson et al. 2020). Chironomids are a notable taxon for bats in tailwaters because many of the other invertebrate taxa that dominate tailwaters are non-insects that do not have terrestrial life stages (e.g., scuds, snails, mussels) and are therefore largely unavailable to bats and other terrestrial predators (Abernethy et al. 2021).

In addition to the availability of aquatic flies, sampling start time was an important predictor for canyon bats and small myotis. Canyon bat activity was greatest early in the evening, whereas small myotis were most active later in the evening. This aligns with previous natural history records of these taxa. Canyon bats are active early in the evening, often before sunset. They rest during the night and forage again at dawn and after sunrise (Ammerman 2012). Yuma myotis peak activity has been recorded as 1–2.5 hour after sunset (Jones 1965) and California myotis activity in southern Nevada, USA, peaks 1–1.5 hour after sunset (O'Farrell et al. 1967). Though our sampling was limited to a 1-hour period (with a median start time of 11 minutes after sunset), there was strong evidence for temporal niche partitioning between canyon bats and small myotis, with each taxa having a distinct diel activity period. Temporal niche partitioning has been widely reported in the animal ecology literature and may reduce negative effects of competing for a shared resource (aquatic flies) thereby facilitating co-existence between species with similar feeding habits (Patterson et al. 2003). Extending acoustic recording to the extent of the full night may provide further insight into variation in bat activity by species and time.

Canyon bat activity also varied seasonally, with activity peaking in August. Canyon bats are most active in the summer, which coincides with warmer air temperatures (Adams 2003). In Big Bend National Park in Texas, USA, the number of volant juvenile bats mist-netted doubled in July compared to the 2 months prior and accounted for 65.8% of foraging canyon bats (Demere 2016). In Grand Canyon, we also saw an increase in canyon bat activity in July and August, coinciding with the 2 months when prey is at a maximal availability. Pregnant canyon bats have been captured in mist nets along the river corridor in May and June (P. B. Holton, U.S. National Park Service, unpublished data). Therefore, the peak activity that we detected for canyon bats in August can likely be attributed to the presence of juveniles foraging during the time of year when there is maximal prey availability.

Vegetation, landscape structure, and noise

Riparian vegetation provides bats with important structural habitat for night roosting, defines travel corridors, and offers cover from wind, light, and predators (Ober and Hayes 2008). However, in our models tall vegetation cover

was not an important predictor of bat activity. This is likely because we sampled solely along a lateral axis (along the river corridor) in a riparian corridor that ranged in width from 0.02–0.41 km of an otherwise wide canyon (the maximum distance between the north and south rim in Grand Canyon is 29 km). Previous research has found that bats track prey along lateral axes but that landscape structure and riparian vegetation have more influence on bat activity than food availability on longitudinal axes (Hagen and Sabo 2011). In a manipulative field experiment where aquatic insect emergence was eliminated over a 12-km reach using a physical barrier, bat foraging activity was reduced as compared to a control reach where aquatic insect emergence was unconstrained (Fukui et al. 2006). Overall, our results support previous findings that prey availability is the primary predictor of bat activity along a river course.

The riparian zone in Grand Canyon has taller riparian vegetation now than it has for at least a century and probably longer (Sankey et al. 2015). Upstream operations of Glen Canyon Dam have more than doubled the areal coverage of woody riparian shrubs and trees since the dam was completed in 1963 (Johnson 1991, Sankey et al. 2015, Durning et al. 2021). Riparian vegetation area is predicted to continue to increase in the coming decades owing to the planned operations of the dam (Kasprak et al. 2021). While bat activity increases with vegetation cover in other systems, the influence of vegetation on bat activity can vary by bat species, vegetation characteristics, and scale (Ober and Hayes 2008). Unlike the models in Ober and Hayes (2008) that implicitly linked vegetation cover and prey availability, our study directly contrasted the effects of prey availability and tall vegetation cover on bat activity. Sampling locations in our study were biased towards well established camps, and these sites may not be representative of vegetation characteristics throughout the canyon. Additionally, many of the habitat functions or attributes that vegetation provides to bats, particularly roosting sites, can also be found in the steep canyon walls and crevices of Grand Canyon. Small myotis and canyon bats roost in rock crevices, and we suggest the abundant crevices found throughout Grand Canyon may render riparian vegetation less important as roosts, but vegetation may still be important to bats on a longitudinal axis from the river as cover (from wind and light) and a source of terrestrial prey.

Physiographic landscape components may be an important determinants of bat activity for species that were underrepresented in our study design. Our acoustic data were biased toward bat species that fly closer to the ground and are thus easier to detect acoustically. Canyon bats and small myotis are low fliers and indeed these species were the most abundant in our survey. In contrast, free-tailed bats (Mollosidae family) were uncommon in our study, likely because they tend to be high fliers and are less likely to be active near the canyon floor.

Community science and data quality

Community science is gaining traction as a tool for data collection and public engagement, especially in freshwater research (Metcalfe et al. 2022). Collaborating with recreational river runners through a community science program enabled us to collect data in a remote riverscape on a spatial and temporal scale that would not have been feasible through traditional scientific field expeditions. Training in sample collection at the start of the season and recurring meetings with participants for equipment resupply during the season provided opportunities for us to hear feedback on the methods and equipment. In turn, these regular meetings with participants allowed us to provide feedback on the quality of data collections and to share insights concerning scientific findings. In addition to disseminating scientific findings in traditional outlets such as journals, we also convey scientific findings directly to project participants via presentations at annual river guide training seminars, by contributing written articles to industry publications, and through mass media coverage of the project including radio and newspaper. Such 2-way communication throughout all phases of the study is critical to successful community science projects (Metcalfe et al. 2022).

The acoutsic detectors we used allowed us to meet our dual objectives of engaging community scientists while also collecting useful scientific data. In particular, participants could view spectrograms and species identifications

in near real-time providing an engaging data-collection experience for river guides and their passengers. Although hardware and software for bat echolocation research are improving rapidly, many of these products do not provide real-time viewing of bat activity data like the Echo-meter we used. Transitioning to different bat acoustic monitoring devices might improve the quality of acoustic data collected, but using devices that lack real-time data viewing would detract from the broader impacts of this community science project.

Different automated species identification algorithms can produce different results (Lemen et al. 2015), which is why manual review and verification of calls by trained experts is necessary (Reichert et al. 2018). Processing the large volume of data that we compiled over 4 years of surveys with 12 acoustic devices was an important consideration in our choice of species identification software. Auto-identification provided a fast, repeatable means of achieving our primary objectives of quantifying the activity patterns of bats. We then followed up with targeted manual examination of records to verify species presence and phenology. Combining large volume processing of thousands of recordings with targeted, expert review of some files produced a tractable dataset for our research questions.

MANAGEMENT IMPLICATIONS

The majority of rivers throughout the world are dammed and this provides an important opportunity for bat conservation. Bats require surface water, and emergent insects are the dominant prey items consumed by some insectivorous bats. Regulated rivers provide both of these essential habitat features. Yet damming rivers and hydropower production leads to altered aquatic ecosystems and these changes can directly affect the activity and distribution of bats and other wildlife. Dam management practices that promote production and diversity of aquatic insect assemblages will likely also benefit conservation and management of bat species that forage in the riparian corridor.

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Sampling aquatic insects and recording bats was conducted in compliance with Grand Canyon National Park Study (GRCA-00273). Community science participants agreed to the use of field-collected data for scientific analyses and publications.

DATA AVAILABILITY STATEMENT

Data generated from this study are available from the United States Geological Survey ScienceBase-Catalog (Metcalfe et al. 2023).

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