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Unlocking the role of beaver in state-transition and their own sustainability in Yellowstone's northern range

Marjorie L. Brooks

Department of Zoology, Southern Illinois University, Carbondale, IL
mlbrooks@siu.edu

Abstract Extirpation of wolves from the Greater Yellowstone Ecosystem (GYE) in the 1920s hypothetically triggered a behaviorally-mediated trophic cascade in which elk (*Cervus elaphus*), released from the fear of wolf (*Canis lupus*) predation, over-browsed riparian zones. Eventually, vast areas of meadow-wetland complexes transitioned to grass-lodgepole systems. The importance of beaver (*Castor canadensis*) in wetland losses has received less attention. Beaver abandoned most of the GYE by the 1950s, possibly due to resource limitations. Researchers from Colorado State University established an experimental system for Long Term Environmental Research in Biology (LTREB) along several streams in the Lamar Valley of Yellowstone sixteen years ago. To evaluate effects of hydrologic changes and elk browsing on productivity of willows (*Salix* spp.) and state transition, they built small experimental dams with browsing exclosures. In 2015, beaver began recolonizing the region. I am investigating how their biologic as well as hydrologic impacts affect the underlying mechanisms of state transition: nutrient cycling, productivity, and stream respiration. I posit that beaver are keystone species, meaning that the sustained recovery of wetland-meadow complexes is unlikely without the higher levels of riparian productivity triggered by the biological influence of beaver.

Introduction

Based on increased growth of riparian vegetation following the 1995 reintroduction of the wolf (*Canis lupus*), researchers hypothesized that wolf extirpation in the 1920s released elk (*Cervus elaphus*) and other ungulates from fear of predation in riparian zones (Painter et al., 2015; Ripple and Beschta, 2004, 2012). Subsequent overbrowsing led to degraded riparian vegetation and a state transition from productive meadow-wetland complexes to dry grasslands (Fig. 1). A lively scientific debate continues about the relative influences on wetland recovery from the wolf-elk trophic cascade, overall declines in elk populations, effects of other browsers, and periodic drought events (Beschta and Ripple, 2013; Creel and Christianson, 2009; Kauffman et al., 2013, 2010). The evidence for both sides of the debate has largely depended on mensurative field studies. Such observational and sampling studies carry tremendous ecological relevance but, because they are fundamentally observational, they face challenges from lack of replication, reproducibility, and strictly controlled reference sites.

Sixteen years ago, David Cooper and Tom Hobbs from Colorado State University established an experimental site for Long Term Environmental Research in Biology (LTREB) in the Lamar Valley, *Understanding controls on state-transition on Yellowstone's northern range*. To evaluate the effects of increased hydrologic delivery of groundwater and elk browsing, they installed a series of experimental dams at three stream sites with adjacent exclosures that prohibit brows-

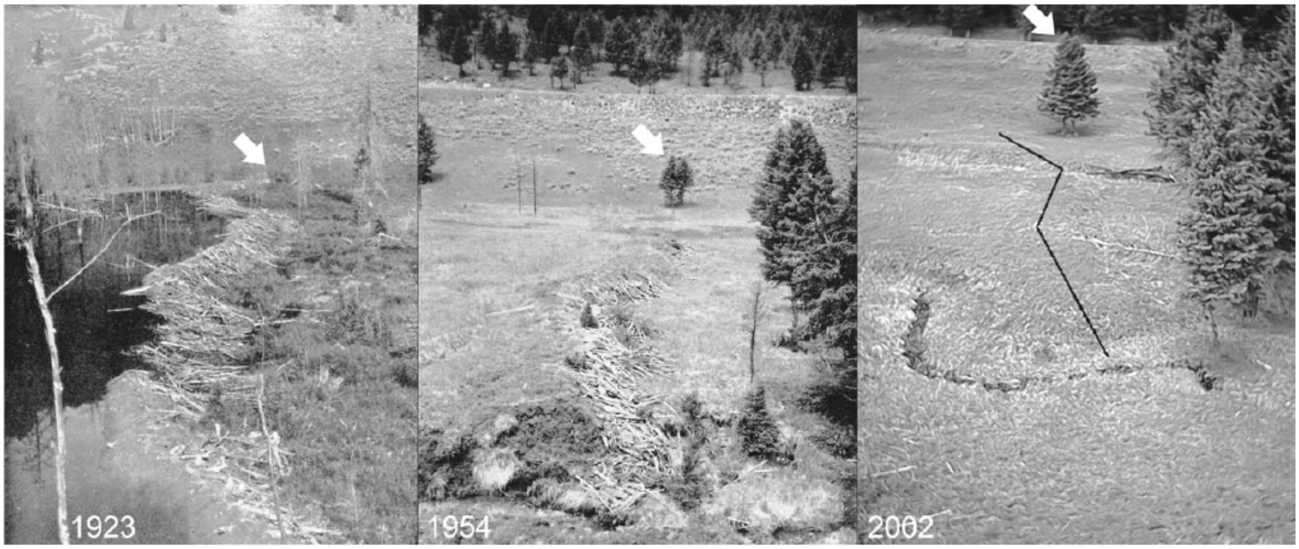

Figure 1. Comparison of historic photos of Elk Creek in the Lamar Valley. In 1923, the beaver dam was more than 100 m long with a robust willow stand (Warren, 1926). The dam had drained and the willows were gone by 1954 (Jonas, 1955). By 2002, a grass and lodgepole pine community entirely replaced the willow-meadow complex. The black line marks the old dam location with the deeply incised stream in the foreground. (From Wolf et al., 2007, Figure 8.)

ing. The experimental dams mimic the influence of beaver (*Castor canadensis*). They and their students show that hydrologic changes, water availability, and drought regimes determine willow growth (Schook and Cooper, 2014) to a greater extent than elk grazing (Marshall et al., 2014, 2013; Wolf et al., 2007). In addition to hydrologic influences, the next logical step is to investigate the biological mechanisms by which beaver alter nutrient cycling, stream metabolism, or system productivity.

By the mid-1950s, beaver populations had declined precipitously throughout the Greater Yellowstone Ecosystem (GYE) and virtually disappeared from the Lamar Valley (Persico and Meyer, 2013). Beaver apparently abandoned because of a combination of overbrowsing and drought events in the 1930s. Without beaver maintenance, spring runoff eventually breached their dams, which dramatically changed wetland-meadow hydrology (Persico and Meyer, 2013; Wolf et al., 2007). Beyond their hydrologic influences, beaver biologically facilitate ecosystem productivity by adding nutrients as feces and transferring woody debris into streams (Fig. 2). Their activity enhances primary production, while promoting higher decompositional rates and nutrient regeneration (Johnston and Naiman, 1987, 1990; Klotz, 1998; Naiman et al., 1994). For example, Naiman and Melillo (1984) found that nitrogen fixation in a stream riffle contributed 4.2% of the nitrogen, but in a similar reach dammed by beaver, fixation contributed 68% of the annual nitrogen budget (Naiman and Melillo, 1984). Although such benefits are well described, dynamic thresholds, chronology of changing system productivity, the magnitude of their influence, and separation of hydrologic from biologic mechanisms are not (arrows between compartments in Fig. 2).

In the past, detection and investigation of the separate hydrologic and biologic processes provided by beaver was impossible because there were no beaver dams to compare to the experimental dams. Starting in 2015, however, beaver conveniently began colonizing streams, below or near the LTREB sites (Fig. 3). LTREB research had not previously included nutrient assessments.

In August 2015, approximately five months after beaver returned to the Yellowstone section of the Lamar Valley, I began a self-funded study to evaluate the fundamental question of whether beaver are

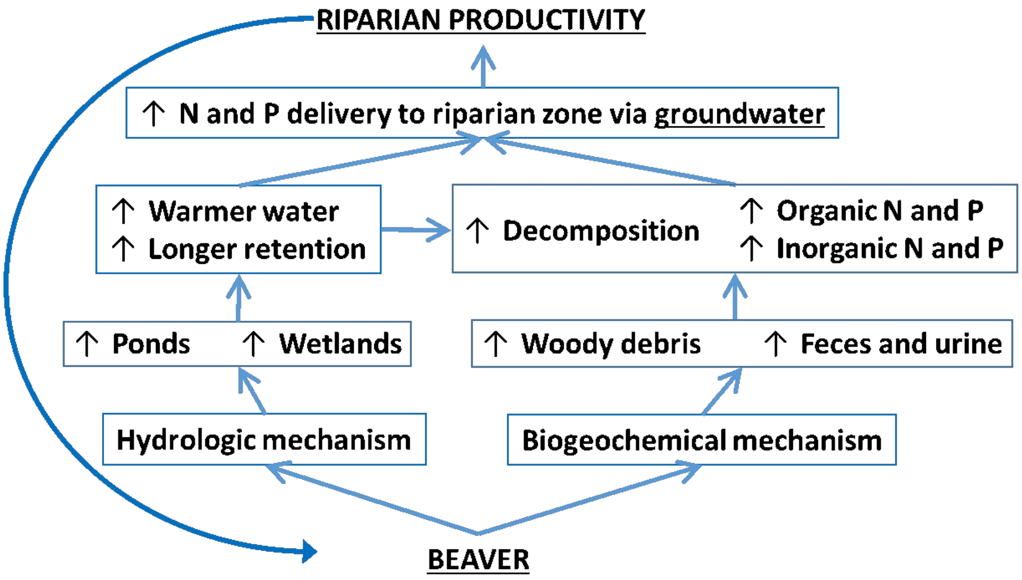

Figure 2. Conceptual model of beaver as keystone species in the state-transition of streams to wetland meadow complexes.

a keystone species, critical to the state-transition from degraded streams to wetland-meadow complexes. David Cooper and N. Thompson Hobbs have included me as a contributor to their LTREB as my sampling complements their long-term monitoring framework.

Beaver immigration presents an unprecedented opportunity in ecology to investigate several important questions about the interplay between the hydrologic and biologic mechanisms. From a conservation standpoint, will the recovery of systems be adequate to sustain viable beaver populations, and to establish historical levels of productivity that will sustain beaver and many wetland-dependent species and fishes (Collen and Gibson, 2000; Hossack et al., 2015; Law et al., 2016)? What timeframe is required for their sustainability? By collecting data from the onset of beaver recolonization, the aims of this research are consistent with Research Needs for the GYE for recovery following wolf reintroduction. My study, which includes temperature monitoring, also provides baseline information for the larger concerns of climatic influences to aquatic and terrestrial habitats of fisheries and wildlife.

Rationale and significance

As in areas fertilized by salmon and river otters (Helfield and Naiman, 2001; Kominoski et al., 2015; Roe et al., 2010), I posit that biological feedback of nutrients mediated by beaver is critical to full system recovery. Unlike otters, beaver seldom defecate onshore. However, their biologic influence on nutrient levels within streams can reach riparian vegetation via surface flooding or lateral seepage of groundwater to the hyporheic zone. My preliminary data collected in 2015 and 2016 from newly established beaver ponds indicate higher N and P concentrations in groundwater beneath riparian zones adjacent to beaver dams than in experimentally dammed streams (Fig. 4). If this pattern holds in further studies, it would represent a **newly discovered mechanism by which alteration of nutrient dynamics within streams by beaver accelerates the transition from elk meadows lacking willows to beaver meadows with vigorous willow growth**. This nutrient-driven process, which occurs in tandem with greater surface flooding around dams and accompanying lateral seepage of groundwater, adds a novel parallel dimension to better-recognized hydrologic effects of beaver (Fig. 2).

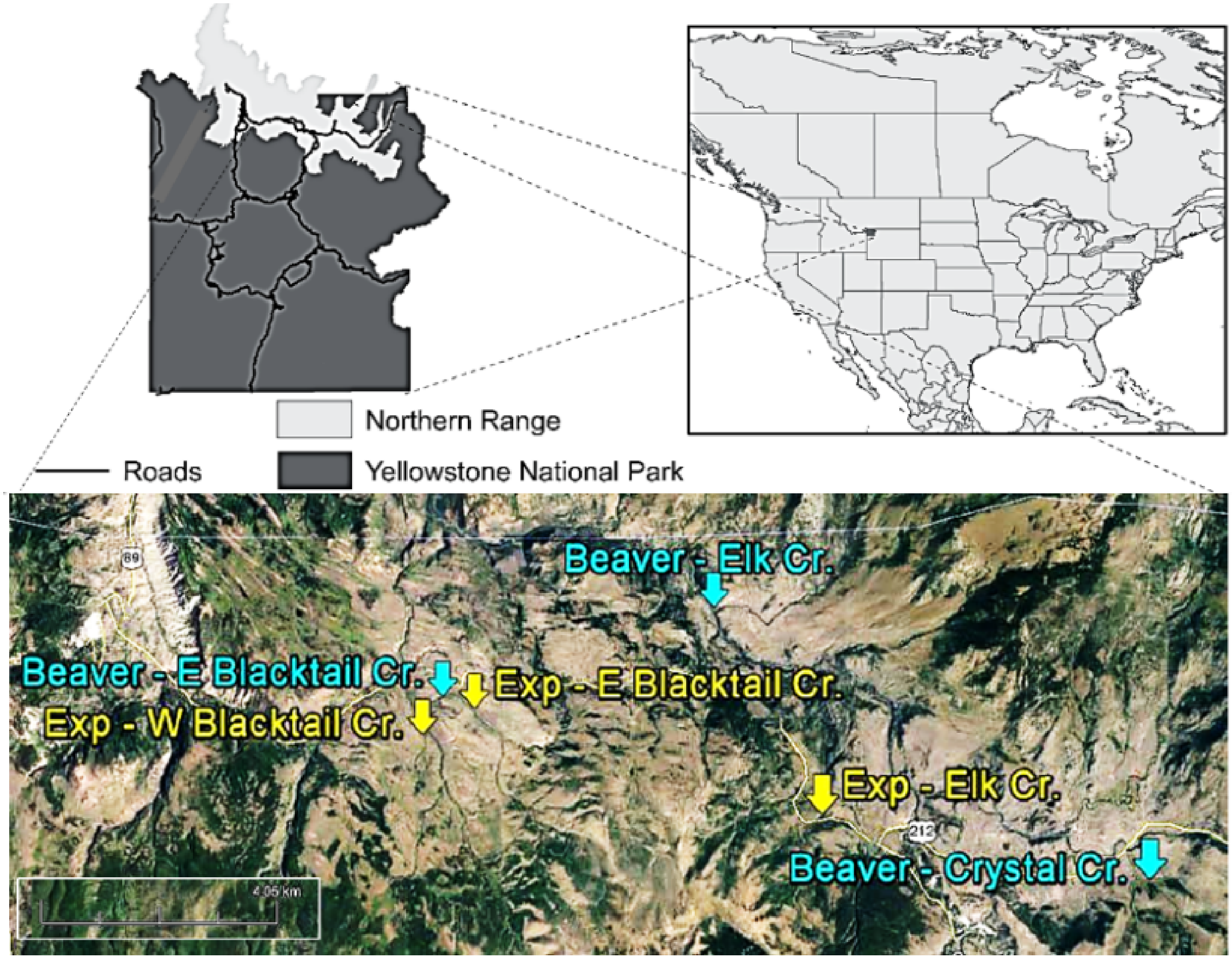

Figure 3. Locations of LTREB experimental dams (West Blacktail Creek, East Blacktail Creek, Elk Creek) and beaver dams (Crystal Creek, Elk Creek, East Blacktail Creek; after Marshall et al., 2014.)

Research questions

1. Do beaver increase the magnitude and rate of nutrient cycling in streams?
2. Does their biologic influence on nutrients and stream metabolism via feces and import of terrestrial woody debris outpace hydrologic influences (i.e. slowed flow, warmer temperatures)?
3. Does nutrient delivery to the roots of riparian vegetation accelerate willow and aspen productivity to levels adequately high to sustain beaver resource needs, and beaver populations?

Coupling the LTREB monitoring with my biogeochemical sampling will allow greater understanding of these questions about ecosystem function and the trajectory of system productivity over time as beaver recolonize the GYE. The steps in the process of characterizing and testing beaver influence include sampling: (1) levels of nutrients and rates of nutrient regeneration and cycling in the streams (Hall et al., 2013, 2016; Kominoski et al., 2015), (2) nutrient levels in groundwater wells within the riparian zone, and (3) growth rates and nutrient levels in leaves of riparian vegetation (Ben-David et al., 1998; Hubbard Jr et al., 2010; Roe et al., 2010).

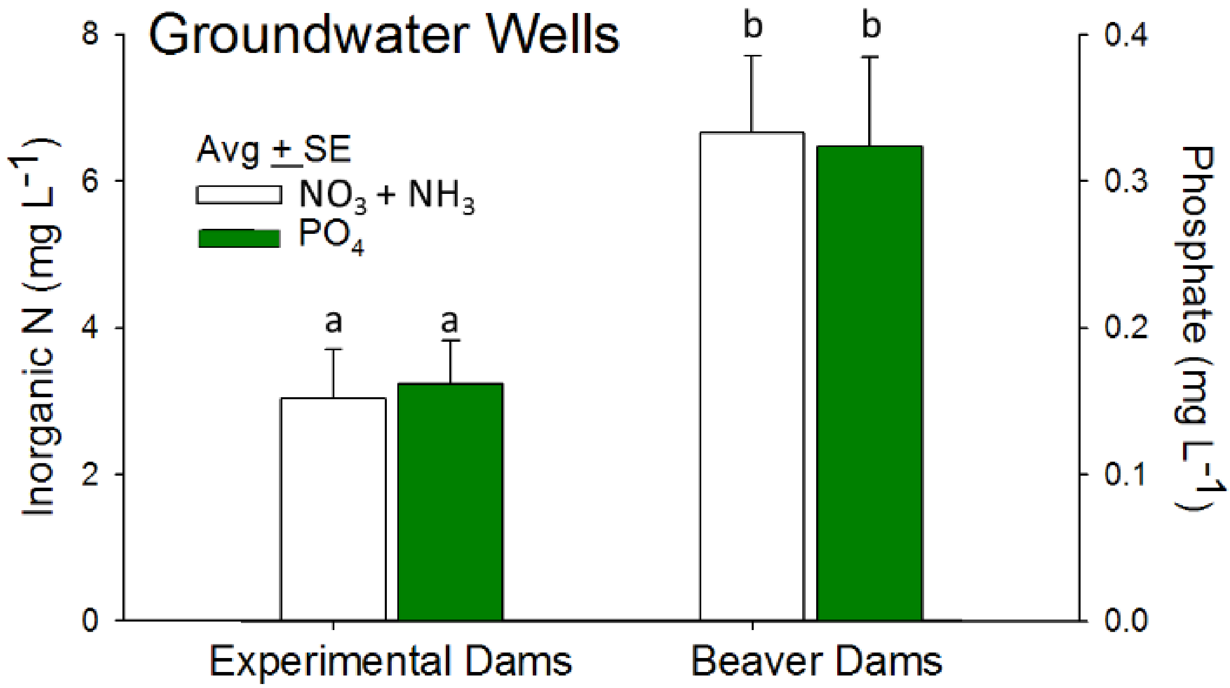

Figure 4. Comparison of total inorganic nitrogen and phosphate collected in groundwater wells adjacent to LTREB experimental dams and beaver dams shown in Figure 3 (Brooks, unpublished data).

Methods

To test the biologic influence of beaver on nutrient concentrations and movement in streams and groundwater, I am my field assistants (Ms. Megan Brown, Ms. Audrey Kross, Mr. William Warner) collected samples from field sites shown in Figure 3 during two sampling bouts from May 20-30 and August 1-10, 2017. Table 1 shows the sampling design and analytes or parameters that we collected.

Samples were collected 50, 10, and 3 m above the dam furthest upstream and 3, 10, and 50 m below the dam furthest downstream. Samples were transported from the field on ice, and stored frozen at -5 °C until analysis. Following thawing, samples were analyzed or stabilized within 24 hours. Aside from on-site parameters (temperature, pH, conductivity, and dissolved oxygen), all analyses were conducted in my laboratory at Southern Illinois University. Samples for stable isotopic analysis will be sent to the UWYO Stable Isotope Facility at the University of Wyoming for analysis. Data for the analysis of gross primary production (GPP), ecosystem respiration (ER), and organic carbon spiraling were collected, specifically two-station oxygen monitoring with concurrent measurements of gas exchange and organic carbon spiraling. Organic carbon spiraling is determined from particulate organic carbon (total dry mass minus ash-free dry mass of fraction > 0.45 μm) relative to dissolved organic carbon (fraction < 0.45 μm; catalytic combustion; Shimadzu TOC-VCSN). Using EPA standard methods, nitrate and phosphate were analyzed by ion chromatography (Dionex ICS 2000, method 300.0), total nitrogen by chemoluminescence (Shimadzu TOC-VCSN), and ammonia and total phosphorus by colorimetric analyses (Hach 5000 spectrometer, P method 365.2, NH_3 method 350.2). Quality assurance and quality checks follow standard QA/QC protocols of duplicates, spikes, and external quality checks and external reference materials (APHA et al., 2005). Stream parameters of temperature, pH, conductivity, and dissolved oxygen were collected on site (HQ40d, HACH multiparameter meter) in streams and existing groundwater wells. To date, neither stream parameters nor nutrients differ significantly between paired pool versus riffle samples (Kruskal-Wallace tests, all $P \geq 0.17$).

Sample Type	No. Samples Collected*	Analytes or parameters
Stream water	6	temperature, pH, conductivity, dissolved oxygen, NO_3, NH_3, PO_4, total P, total N, δ13C, δ15N, C:N ratio, %C, %N, particulate and dissolved organic carbon
Well water	7 to 12	
Sediments	6	NO_3, NH_3, PO_4, total P, total N, δ13C, δ15N, C:N ratio, %C, %N, organic matter
Willow shoots, leaves	6	total P, total N, δ13C, δ15N, C:N ratio, %C, %N
Stream metabolism	1	GPP, ER, and organic carbon spiraling

Table 1. Samples collected at field sites in the Lamar Valley, Yellowstone National Park in 2017.

Statistical analyses

Statistical analyses include Bayesian network models for the strength of relationships in Figure 2 (Ayre and Landis, 2012; Raiho et al., 2015). For hypothesis testing of differences in system productivity between undammed reaches, experimental dams and beaver dams, I will use permutational multivariate analysis of variance (PERMANOVA; PRIMER software ver 7.0.11, PERMANOVA, 1.0.5; PRIMER-E; Anderson, 2001) and non-metric multidimensional scaling with Akaike Information Criteria adjusted for variance in sample size (AICc). For inference, I will use permutational distance-based linear modeling (DistLM; multivariate multiple regression; Anderson et al., 2004; Kraft et al., 2011). I will use Bayesian inverse modeling to estimate GPP and ER (Hall et al., 2016).

Preliminary Results

Sample analyses and statistical analyses are on track with my initial timeline (Table 2). Preliminary results show that both phosphate and nitrogenous nutrients are higher in streams inhabited by beaver. Beaver abandoned one field site sometime over the 2016-2017 winter. Nutrient levels there are intermediate.

Conclusions

Relative to my research questions, preliminary results support the probability that beaver increase the magnitude of nutrient cycling in streams, and thus, that their biologic influence outpaces hydrologic influences of dam building alone (i.e. slowed flow, warmer temperatures). Neither all sample analyses nor the network modeling are complete, so I cannot yet provide evidence whether or not beaver increase rates of nutrient cycling or increase stream metabolism via feces and import of terrestrial woody debris. Regarding my final question, ”Does nutrient delivery to the roots of riparian vegetation accelerate willow and aspen productivity to levels adequately high to sustain beaver resource needs, and thus, their own population?” I expect that my data will provide some insights; however, I cannot yet develop robust inferences based on the preliminary findings.

Acknowledgments

I thank my field assistants Megan Brown, Audrey Kross, and William Warner who weathered sometimes challenging field conditions with good cheer. Mr. Dan Kotter, the doctoral candidate who leads the current field research at the Cooper and Hobbs LTREB, provided logistical support for field sampling as well as invaluable conceptual insights about the ecosystem. I thank Dr. David Cooper and Dr. Tom Hobbs in particular for their generosity in providing me access to their field sites and resources. Conversations with Dr. James Halfpenny and his allowing us to dominate space every night in the Tracker Center for lab analyses have been essential to the success of our endeavors.

	20 - 30 May 2017	June - July 2017	1-10 Aug 2017	12 Aug -Oct 2017	Nov - Jan 2018	Feb- March 2018	17 March 2018
Field sampling	X						
Laboratory analyses		X					
Field sampling			X				
Laboratory analysis				X			
Data analysis		X			X		
Write up results					X	X	
Submit report & paper for publication							X

Table 2. Project timeline.

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