AQUATIC-TERRESTRIAL CONNECTIVITY IN A WILDERNESS WATERSHED: DO EMERGING STREAM INSECTS FUEL RIPARIAN FOOD WEBS FOLLOWING WILDFIRE?

M.S. Research Proposal

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Abstract
Wildfire has the potential to alter many land-water linkages, yet relatively few studies have addressed its influences on stream ecosystems or the vectors of aquatic-terrestrial connectivity. We propose to investigate the mid-term effects of wildfire on several key land-water linkages in the Big Creek Watershed, located in the Frank Church 'River of No Return' Wilderness of central Idaho. We hypothesize that wildfire may serve to amplify aquatic-terrestrial connectivity via a number of direct and indirect mechanisms. The study described here will investigate potential influences of fire on the flow of energy from aquatic to terrestrial habitats via the emergence of adult insects from streams, while a companion study proposed by Dr. Jeff Braatne (riparian ecologist, University of Idaho) will research the effects of fire on plant and invertebrate inputs from land to water. We will test a series of specific hypotheses at sites with varying fire history using direct measurements of aquatic-terrestrial resource fluxes, predator populations and diets, and food web structure across a continuum of stream sizes. We will couple this with the use of the natural abundance of carbon stable isotopes to quantify the effects of fire on the reciprocal flow of energy between aquatic and terrestrial food webs. Together, we expect these investigations will reveal natural dynamics of land-water linkages following wildfire, enhance interpretation of long-term monitoring data from the study area, and set the stage for future collaborative ecosystem research in the Big Creek Watershed.

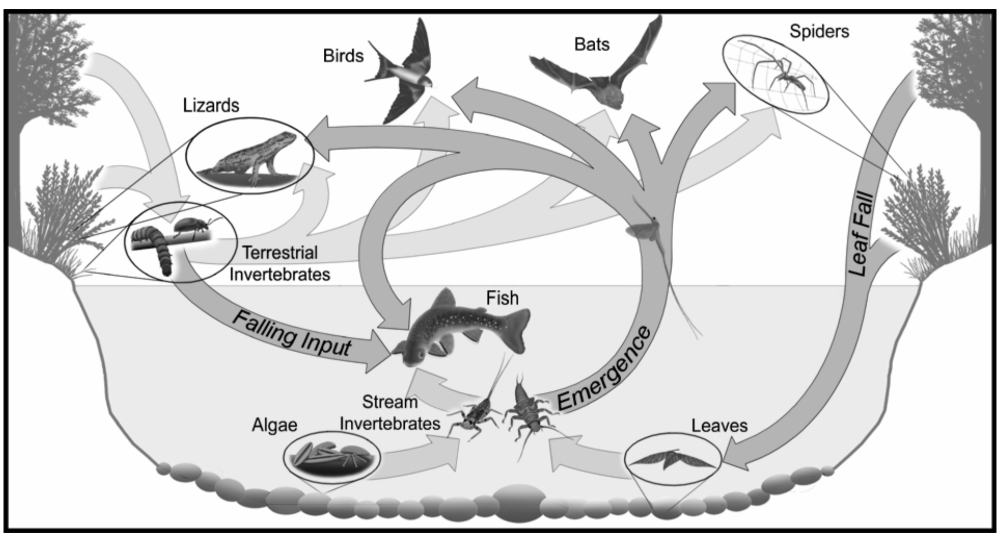

Figure 1. A generalized diagram showing reciprocal flows of invertebrate prey and inputs of plant material (dark arrows) that have direct and indirect effects in stream and riparian food webs (from Baxter et al. 2005).

Introduction
Streams and rivers are closely linked to their adjacent riparian zones and upland habitats by flows of materials and the movement of organisms. In the past, terrestrial environments have been perceived as the more productive donors "feeding" less productive stream ecosystems. For example, ecologists have long recognized the importance of land-to-water fluxes of inorganic and organic materials like nutrients, leaves, and woody debris (Minshall 1967, Likens and Bormann 1974, Hynes 1975), and

new work has highlighted the role of terrestrial invertebrates that fall into streams and become prey for fish (Wipfli 1997, Nakano et al. 1999, Baxter et al. 2005; Figure 1). However, recent research has also demonstrated that reciprocal flows of energy and nutrients from water to land can feed terrestrial organisms and strongly influence the structure and function of riparian ecosystems. Though most of this research has focused on the transfer of marine-derived nutrients from streams to land via salmon carcasses (Ben-David et al. 1998, Helfield and Naiman 2001, Gende et al. 2002), studies have also demonstrated that emergence of adult insects from streams can constitute a substantial export of energy to terrestrial food webs, fueling consumers such as birds, bats, lizards, and spiders (Nakano and Murakami 2001, Power et al. 2004, Baxter et al. 2005; Fig. 1).

As a result of such connectivity, streams and their watersheds are coupled in their responses to both human-driven and natural disturbances. Wildfire is among the most important disturbances in watersheds of the western United States. Fire has the potential to alter all of the land-water linkages described above, yet relatively few studies have addressed its influences on stream ecosystems or the vectors of aquatic-terrestrial connectivity (Bisson et al. 2003, Dwire and Kauffman 2003). Minshall et al. (2004) categorized stages of watershed response and recovery following fire as (1) immediate (the time of active burning to a few days after); (2) short-term changes (a few days to the beginning of spring run-off); (3) mid-term changes (from spring runoff of the 1st post-fire year to sometime beyond the 10th year); and (4) long-term changes (occurring decades or centuries later).

We propose to investigate the mid-term effects of wildfire on several key land-water linkages in the Big Creek Watershed, located in the Frank Church 'River of No Return' Wilderness of central Idaho. Results of previous research in this region by Dr. Wayne Minshall and colleagues (e.g., Minshall et al. 1997, Minshall et al. 2001, Minshall 2003, Minshall et al. 2004, Robinson et al. 2005) have led us to hypothesize that wildfire may serve to amplify aquatic-terrestrial connectivity via a number of direct and indirect mechanisms. The study described here will investigate potential influences of wildfire on the flow of energy from aquatic to terrestrial habitats via the emergence of adult insects from streams, while a companion study proposed by Dr. Jeff Braatne (riparian ecologist, University of Idaho) will research the effects of fire on plant and invertebrate inputs from land to water.

We will test a series of specific hypotheses (see below) at sites with varying fire history using direct measurements of aquatic-terrestrial resource fluxes, predator populations and diets, and food web structure across a continuum of stream sizes. We will couple this with the use of the natural abundance of carbon stable isotopes to quantify the effects of fire on the reciprocal flow of energy between aquatic and terrestrial food webs. Together, we expect these investigations will reveal natural dynamics of land-water linkages following wildfire, enhance interpretation of long-term monitoring data (collected by Dr. Minshall and colleagues), and set the stage for future collaborative ecosystem research in the Big Creek Watershed.

Hypothesis 1*: *Biomass of stream insect larvae will be higher at burned than unburned sites. Though many of the immediate and short-term effects of wildfire might drive decreases in stream macroinvertebrate production, a number of mid-term effects of wildfire may contribute to greater biomass of benthic insect larvae at burned versus unburned sites (Minshall et al. 1989). For example, fire may increase algal production due to greater sunlight penetration, higher temperatures, and delivery of inorganic nutrients (nitrogen, phosphorous) to the stream (Spencer and Hauer 1991, Robinson et al. 1994). In turn, this may fuel greater production of herbivorous stream insect larvae (Minshall 2003). In addition, the re-growth of riparian vegetation following a fire is likely to include proportionately more herbaceous plants and deciduous shrubs and trees than might have been present pre-fire. Consequently, there may be greater delivery of more labile plant material to streams at burned versus unburned sites, and this material (combined with in-stream sources of detritus) may drive increased production among detritivorous stream insect larvae (Minshall 2003). Regardless of the exact mechanism involved, such effects are likely to be modulated by the intensity of wildfire, as well as the size of the stream and the consequent physiognomy of the stream-riparian interface. For example, if fire did not burn riparian vegetation intensely, mid-term effects on sunlight penetration and plant litter inputs could be minimal. Likewise, the consequences of altered litter inputs or increased sunlight might be strong in small streams but undetectable at larger-order sites. In general, however, pre- and post-fire data collected from sites within the Big Creek Watershed (Minshall et al. 2003) and elsewhere in the Middle Fork of the Salmon basin (Minshall et al. 2001) suggest that macroinvertebrate biomass has increased as a mid-term response to wildfire. A better understanding of this response is required if we are to investigate its consequences for aquatic-terrestrial linkages.

Hypothesis 2*: *Flux of adult insects emerging from streams will be higher at burned than unburned sites. If wildfire drives a mid-term increase in the biomass of benthic stream insect larvae, it is likely that this will be accompanied by greater biomass of adult insects (Fig. 2) emerging from burned versus unburned streams. However, we are aware of no study that has investigated this possibility. The timing of emergence differs among individual insect taxa and is strongly influenced by stream temperature (Vannote and Sweeney 1980). Total community emergence from temperate streams typically peaks in early summer, but also provides a low-level flux to the riparian zone from autumn to spring (Baxter et al. 2005). Emergence often occurs in large pulses (e.g., Sweeney and Vannote 1982) that can be easily missed, so measuring total emergence requires frequent sampling. In addition to increasing the biomass of stream insect larvae, the influences of fire may also alter the taxonomic composition of the assemblage (e.g., Mihuc and Minshall

Figure 2. A combination of factors may drive mid-term increases in the production of insect larvae in streams following wildfire. In turn, this is predicted to result in greater emergence of adult insects like this mayfly to riparian and upland areas.

1995). In concert with shifts in stream temperature regime, this could result in marked changes in the timing, as well as the magnitude, of emergence. Again, we expect these shifts could be mediated by both stream size and the intensity of the burn.

Hypothesis 3: Energy flow from streams to riparian food webs will be greater, and terrestrial predators that specialize on capturing emergent stream insects will be more abundant, at burned than unburned sites. If wildfire results in a mid-term increase in the flux of adult stream insects to riparian areas, what consequences might this have for the suite of terrestrial predators present? Emerging stream insects serve as prey for a host of riparian consumers, including birds, bats, amphibians, lizards, beetles, and spiders, and can contribute anywhere from 25-100% of the energy or carbon to such predators (Fig. 1; Baxter et al. 2005). For example, Nakano and Murakami (2001) reported that aquatic insects made up 26% of the total annual energy budget for the entire bird assemblage in a watershed of northern Japan. Moreover, they found that from autumn to spring when terrestrial prey were scarce, emergent insects made up 50-90% of the monthly energy budget for winter-resident birds. Likewise, guilds of web-weaving and ground-dwelling spiders have been shown to derive the majority of their carbon from emerging stream insects (Power and Rainey 2000, Collier et al. 2002). Consequently, we hypothesize that increased emergence will result in increased flux of stream-derived energy to consumers in riparian food webs.

If energy flow to riparian consumers is higher at burned sites, we expect to observe greater abundance of those consumers that specialize on capturing emergent insects at those locations. However, differences in abundance are most likely to be detected among predators with lower mobility. Flying predators like birds and bats are likely to perceive and respond to variation in emergence at larger scales than those that must crawl, such as amphibians or spiders (Power and Rainey 2000). Consequently, though we expect occurrence of some birds or bats to be greater at burned than unburned sites, we may be most likely to detect a response among consumers like spiders and amphibians. In particular, spiders of the family Tetragnathidae (Fig. 3) build horizontal orb webs in riparian zones and specialize in capturing emergent insects. Studies have shown that their abundance tracks reach-scale variation in emergence (Kato et al. 2003, Baxter et al. 2004), so we hypothesize that they will be more abundant at burned than unburned sites.

Figure 3. Spiders of the family Tetragnathidae live in riparian zones throughout the world and build horizontal orb webs specialized for capturing adult insects that emerge from streams. They are predicted to increase due to indirect effects of wildfire.

Study Design and Methods

***Study Design* –** The working hypotheses described above will be tested using measurements at sites of varying stream size and wildfire history/intensity. These will include Dr. Minshall's long-term study sites (Cliff and Cave Creeks [intense burn], Rush and Pioneer Creeks [cooler-wet burn], Goat and Cougar Creeks [unburned], as well as additional sites within the Big Creek Watershed (e.g., Burnt, Doe [65 yr old fire] and Lewis Creeks) selected in consultation with Drs. Minshall and Braatne to achieve sufficient study replication (minimum of n = 3 per stream size and fire intensity, yielding a total of 18 different study sites) representative of the range of stream sizes, fire history, and intensity within the watershed. These data will be integrated with Dr. Minshall's long-term monitoring results, as well as data from the studies proposed by Dr. Braatne, in order to test our overall hypothesis that land-water connectivity is amplified by wildfire. Results from the proposed studies will aid in interpreting the long-term pre and post-fire monitoring data, which by necessity involved a smaller number of sites and data on fewer parameters.

***Methods* –** At each of the sites we will collect data on a suite of physical and biological parameters in a manner consistent with protocols for the long-term monitoring efforts (see Davis et al. 2001, Minshall et al. 2003 for details). This will include sampling the biomass and taxonomic composition of stream benthic macroinvertebrates, as well as biomass of benthic organic matter and periphyton. These data will allow us to address hypothesis #1 above, but will also complement vegetation and plant litter input data from the studies proposed by Dr. Braatne.

To test hypothesis #2, we will collect data at each site on composition and biomass of adult aquatic insects emerging from the stream. These methods will generally follow previous studies by Baxter and colleagues (Baxter et al. 2004, in review). Insect emergence from each study reach will be sampled using four 1-m^2 floating emergence traps (50 cm high, 0.5 mm-mesh) set in the stream and deployed for 4 d every two weeks. Insects will be removed from traps using an aspirator tube and vial of ethanol. This sampling will be performed continuously from late-spring through early-fall (May-Oct) of the first study year. Winter and early spring sampling will also be conducted 2-3 times. The latter may be possible at only a subset of sites, depending on accessibility.

Addressing hypothesis #3 will require surveys of terrestrial predators, as well as collection of samples for stable isotope analysis. In the first year of the study, we will conduct surveys of riparian spiders at each site. In each study reach, we will select a 30-m transect along one bank that is representative of the riparian habitat. Spiders will be sampled along this transect in mid- to late-summer when they have reached peak abundance, and collection will be conducted at night (using a floodlight, forceps, and glass vials), when spiders are most active and visible (Kato et al. 2003). Also at this time, five pitfall traps will also be positioned along each reach and deployed for 48 h to sample ground-dwelling spiders. Spiders will be counted in the laboratory, adult spiders will be identified to genus and sex identified, and immature spiders will be sorted to Family. Also in the first year of the study, we plan to collect pilot data on occurrence and foraging by other terrestrial predators such as birds, bats, lizards and amphibians. As described by Dr. Braatne in his companion proposal, this effort will involve collaboration with Drs. Dave Delehanty (avian ecologist, ISU) and Chuck Peterson (herpetologist, ISU).

Hypothesis #3 is also linked to our overarching hypothesis that the mid-term effects of wildfire amplify connectivity between aquatic and terrestrial food webs. In collaboration with Drs. Braatne, Delehanty, and Peterson, we plan to test this idea making complementary use of diet analysis and stable isotope techniques (Peterson and Fry 1987). Relative contributions of in-stream versus terrestrial carbon sources to the diets of terrestrial and aquatic consumers will be estimated using carbon stable isotope ratios and a two-source mixing model (Doucett et al. 1996). As described above, we expect that terrestrial predators like spiders and birds will derive proportionately more of their energy from aquatic sources at burned vs. unburned sites. Likewise, we anticipate that fish will derive proportionately more of their carbon from land (either through direct input of terrestrial invertebrates or indirectly through plant litter that fuels stream invertebrate production) at burned vs. unburned sites. In addition to samples for stable isotope analyses (i.e., whole invertebrates, tissue from vertebrates), we plan to collect diet contents from spiders (i.e., web contents), amphibians, birds, and fish. These data will aid in verification and interpretation of results from isotope analysis. Diet contents will be preserved, and then sorted and identified in the lab.

Potential Significance of Results

Informed management policies regarding the role of wildfire in watersheds requires improved understanding of mid to long-term responses to this natural disturbance. Study of such effects in wilderness watersheds is important to set the context for evaluating the impacts of fire in human-dominated landscapes where natural fire regimes have been altered by suppression and land-cover change. The proposed study will be the first to investigate the influence of fire on the flux of material and organisms between aquatic and terrestrial food webs. This work should make a significant contribution to our understanding of the coupled responses of aquatic and terrestrial ecosystems to wildfire, as well as to other natural and anthropogenic disturbances.

Integration of Research Efforts

As described above, the proposed study will be closely integrated with Dr. Minshall's long-term research in the Big Creek Watershed, as well as the companion study proposed by Dr. Braatne. As pointed out by Dr. Braatne in his proposal, hypothesis #3 and associated objectives have been put forth with the intent to capture the interest and talent of additional researchers from the University of Idaho and Idaho State University, as well as other regional institutions. The findings from these studies will be used in crafting competitive grant proposals in the coming years. In this manner, we hope to establish a framework for long-term ecosystem studies in the Big Creek Watershed.

Proposed Study Timeline (2005-2006)

March 2005: Additional discussions w/Drs. Braatne & Minshall to advance study design
April 2005: Fly into Taylor to select additional study sites w/Drs. Braatne & Minshall
May-Oct 2005: Field sampling in Big Creek Watershed, plus processing samples in fall
Winter 2005: Winter sampling, process samples, analyze and report first year's data

Spring 2006: Annual report, write competitive grants to NSF/USDA/UNESCO
May-Oct 2006: Field sampling in Big Creek Watershed, plus processing samples in fall
Winter 2006: Process samples and analyze second year's data

Spring 2007: Complete analysis & report, manuscript preparation & MSc thesis defense
Summer 2007 (& Beyond): Continue interdisciplinary research within Big Creek Basin

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Proposed Study Budget (2005-2006):

To conduct the proposed study, funding is required for masters-level graduate student stipend and fees (2 years), transportation, food and lodging, lab sample and stable isotope analyses, misc. field supplies, and equipment (2 field seasons). The DeVlieg-Taylor Ranch Graduate Research Assistantship would cover the graduate student stipend and fees. As a new faculty member at Idaho State University, I will use my start-up resources to cover a month of my own summer salary per year, pay for travel, and obtain the field equipment needed for this study. I am also in the process of using start-up funds to complete renovations on the ISU Stream Ecology Center. This facility will be fully equipped for processing the study samples (with exception of stable isotope analysis), performing data analysis, and publishing our findings. Stable isotope analysis will be performed at the University of Idaho's facility. As noted above, our intent will be to use the data derived from these proposed UI/ISU interdisciplinary studies to obtain long-term ecological research funding from national and international competitive grant programs (NSF, USDA, & UNESCO).

		Year 1	Year 2	Summary
Salaries				
	MSc. Student	14400	14400	28800
	Field Assistant	3000	3000	6000
Fringe		1550	1550	3100
Sal & Fnge		18950	18950	37900
Fees/Tuition	Grad Student Fees	5040	5040	10080
Oper. Expenses				
	Field supplies	500	500	1000
	Stable Isotope Analysis	2000	2000	4000
	Travel (auto/plane)	1000	1000	2000
	Food & Lodging	1000	1000	2000
Total		28490	28490	56980

Funding request:
DeVlieg-Taylor Ranch Graduate Fellowship ($18,500/year @2 yrs) $37,000

Other funding support obtained:
Idaho State University $20,000

Total project funds: $57,000

Biographical Sketch

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a. Professional preparation

University of Oregon	Biology & Geology	B.S. 1993
University of Montana	Biology & Ecology	M.S. 1997
Oregon State University	Fisheries Biology	Ph.D. 2002
Colorado State University	Ecology	Postdoctoral Researcher 2002-04

b. Appointments Assistant Professor Idaho State Univ. 2004-present

c. Publications - Five Publications Related to Proposal

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(2): in press.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85:2656-2663.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, H.W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52: 483-498.

Baxter, C.V. and F.R. Hauer. 2000. Geomorphology, hyporheic exchange and selection of spawning habitat by bull trout (*Salvelinus confluentus*). *Canadian Journal of Fisheries and Aquatic Sciences* 57: 1470-1481.

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d. Five Other Publications

Baxter, C.V., F.R. Hauer and W.W. Woessner 2003. Measuring groundwater-stream water exchange: new techniques for installing mini-piezometers and estimating hydraulic conductivity. *Transactions of the American Fisheries Society* 132: 493-502.

Torgersen, C.E., C.V. Baxter, H.W. Li, and B.A. McIntosh. In press. Landscape influences on longitudinal patterns of stream fishes: spatially continuous analysis of fish-habitat relationships. *In* R. Hughes, L. Wang, and P. Seelbach, editors. *Influences of landscapes on stream habitats and biological communities*. American Fisheries Society, Bethesda, Maryland, USA.

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d. Examples of Synergistic Activities

1. Visiting Postdoctoral Fellow, *Japanese Society for the Promotion of Science (JSPS)* - During summer 2002, collaborated with Japanese ecologists and Dr. Kurt Fausch to conduct field experiment study for NSF sponsored project.. Presented seminars and interacted with scientists at universities and government agencies in Japan. Invited by editor of *Freshwater Biology* to publish special review article on stream-forest food web connectivity.

2. Cooperated with Dr. Kurt Fausch to successfully gain NSF REU (Research Experiences for Undergraduates) grant for research in Japan, and mentored student Scott Laeser (U. of WI-Madison) in research on riparian spiders.

3. Invited Reviewer and Advisory Committee Member – U.S. Fish and Wildlife Service proposed Critical Habitat Rule and Draft Recovery Plan for Bull Trout – 2003-04.

4. Invited Reviewer – *Aquatic Sciences, Ecological Applications, Ecology of Freshwater Fish, Ecosystems, Environmental Management, Hydrological Processes, Journal of the North American Benthological Society, Transactions of the American Fisheries Society, North American Journal of Fisheries Management, Northwest Science*.