

AN ABSTRACT OF THE THESIS OF

Alexander Mark Farrand for the degree of Master of Science in Fisheries Science presented on June 4, 2004.

Title: Effect of Adult Aquatic Insect Life Histories on Return to Lookout Creek, H.J. Andrews Experimental Forest, Oregon

Abstract approved:

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Aquatic insects that emerge out of streams to mate represent a potential energy flux to terrestrial food webs. The relative success of an individual aquatic adult insect is whether it survives long enough to produce offspring, i.e. mate and return to the stream to oviposit eggs. Some characteristics of the adult stage of aquatic insects are thought to be responses to aerial and terrestrial predation from riparian insectivores. These characteristics and behaviors may result in differential numbers of returning individuals to the stream .

In summer 2001 we measured emergence and return of adult aquatic Ephemeroptera, Plecoptera and Trichoptera at Lookout Creek, a 4<sup>th</sup> order western Oregon montane stream located in H.J. Andrews Experimental Forest. As a group, Plecoptera had the highest proportion of returning adults ( $P\{\text{return}\} = 0.37$ ), Ephemeroptera the second highest ( $P\{\text{return}\} = 0.28$ ), and Trichoptera the lowest

( $P_{\text{return}}=0.18$ ). The range in return proportion among families within an order was large but among species within a family or genus they were surprisingly similar.

Concurrently, we assessed the associations between adult behavior, specifically diel activity, the longevity of the adult stage, and length of emergence period with adult return to the stream. Six out of seven Trichoptera species were nocturnal at our study site, but only two out of six Plecoptera and four out of seven Ephemeroptera exhibited higher activity at night than during the day. Calculated values of diel activity at the species level ranged widely, even among congenics. Simple linear regression of our measure of diel activity on return proportion was moderately significant ( $R^2 = 0.42$ ,  $p < 0.02$ ) at the family level but the relationship was weak at the species level ( $R^2 = 0.22$ ,  $p < 0.08$ ).

As expected, Trichoptera species averaged longer adult stages than Plecoptera (1-4 weeks vs. 0.5-1.5 weeks). Also, most Trichoptera species had extended emergence periods of 8 weeks or longer, while many Plecoptera and all but one Ephemeroptera had emergence periods of 6 weeks or shorter. Overall, species with shorter adult life stages had greater return proportions, but this relationship was marginally significant ( $R^2 = 0.23$ ,  $p < 0.05$ ). A stronger negative relationship existed between emergence period length and return proportion ( $R^2 = 0.34$ ,  $p < 0.02$ ). The similarity in return proportion in closely related species indicates that factor(s) producing differential return numbers are important at the genus and species level. However, similarities in diel behavior, adult longevity, or emergence period durations did not occur among closely related species. We conclude, therefore, that despite

some evidence of a relationship between the three life history dimensions and return proportion, the absence of similar patterns within or among taxa shows that other factors are more important influences on determining how many insects survive to oviposition.

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Effect of Adult Aquatic Insect Life History  
on Return to Lookout Creek, H. J. Andrews  
Experimental Forest, Oregon

By

Alexander Mark Farrand

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Alexander Mark Farrand, Author

## ACKNOWLEDGEMENTS

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to its fullest is an inspiration to everyone who knew him, and there are many. It is to him that I dedicate this work.

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The last word in ignorance is the man who says of an animal or plant: 'What good is it?' If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering.

- Aldo Leopold, in *The Round River* 1953

# **Effects of adult aquatic insect life histories on return to Lookout Creek, H.J. Andrews Experimental Forest, Oregon**

## **Introduction**

Aquatic insects emerging out of the water represent a possible food source for many riparian insectivores. Terrestrial consumption of aquatically derived energy in the form of aquatic insects can be considered a “spatial subsidy” (Polis et al. 1997), whereby an ecosystem’s biological production is sustained in part from energy inputs from adjacent biological systems. The level of production within the receiving system is higher than it would be without these inputs. There are numerous energy pathways that link both the aquatic and its adjacent terrestrial ecosystem in cross-boundary food webs (Power and Rainey 2000). The relationship between streams and adjacent riparian zones has generally focused on the transfer of terrestrial energy to aquatic food webs, e.g. detrital leaf litter inputs to small headwater streams (Vannote et al. 1980, Webster and Benfield 1986), dissolved nutrients from run-off (Likens and Bormann 1974), and terrestrial invertebrates as a food source for fish (Nakano et al. 1999, Wipfli 1997). Recent research forays into aquatic energy subsidies to terrestrial food webs, notably salmon carcasses supporting terrestrial food webs (Willson and Halupka 1995, Bilby et al. 1996) have reversed this trend to some extent, but gaps in our knowledge remain. In particular, energy flux in the form of emerging aquatic insects has not been adequately quantified.

A typical life history of stream-dwelling insects is to develop from egg through several larval instars in the lotic environment, then leave the water as an adult to find suitable mates in the terrestrial system. The period of emergence can last from a few weeks to several months for a given taxa. After mating successfully, many females deliver their fertilized eggs directly back into the stream to start the cycle anew. The majority of them achieve this by dimpling their lower abdomen into the water to extrude their egg mass, but other oviposition behaviors, such as diving beneath the surface and attaching eggs to the substrate, are also common. Energy reserves of adults generally do not last beyond one or two egg batches laid in the water and both male and female aquatic insects usually succumb shortly thereafter (Clifford et al. 1979). The entire adult life stage can last from just a few hours in some taxa to several months in others (Wallace and Anderson 1996). During this time they are vulnerable to predation by terrestrial insectivores such as birds, bats, and spiders, or to inhospitable climatic conditions, such as extreme heat or cold or heavy rain (Hynes 1976, Brittain 1982).

Three exclusively aquatic insect orders in particular are known to exhibit this life history type almost without exception: the Ephemeroptera (mayflies), Plecoptera (stoneflies), and the Trichoptera (caddisflies) – also known as the EPT orders. By measuring densities of EPT insects at the water surface as they move across this boundary in both directions – first to leave the water and find mates in the riparian corridor and then to return and deposit eggs in the water - the proportion of individuals returning to the stream from those that emerged can be estimated. Conversely, these

estimates provide a measure of the relative contribution of different EPT taxa to riparian food webs. Thus, return proportion represents those individuals of a population surviving the adult stage long enough to complete the mating process.

The importance of aquatic prey sources in the maintenance of riparian food webs has been noted in investigations into the prey availability (Busby and Sealy 1979, Raley and Anderson 1990), habitat use (Brigham et al., 1992, Whitaker et al. 2000, Grindal 1998, St. Louis et al. 1990), and behaviors of common riparian insectivores such as birds (Smith et al. 1998), bats (Fenton and Morris 1976, Frenckell and Barclay, 1987), and spiders (Sanzone et al. 2003). Only recently have attempts been made to quantify this flux. Gray (1993), for example, reported peak bird foraging activity coinciding with peak emergence of aquatic insects along prairie streams in Kansas. Along a stream in northern Japan, 25.6% of birds' energy budget consisted of aquatically derived prey, and the energy flux in terms of invertebrate biomass out of the water exceeded arthropod inputs to the stream (Nakano and Murakami 2001). Brigham (1990) reported that large trichopterans made up 61.6 % of a bat's and 64.1 % of common nighthawk's diet although they represented only 13.3 % of available insect prey. Spiders have also been shown to be significant consumers of aquatic insects. In a desert riparian system in Arizona, spiders obtained 100% of their carbon and 39% of their nitrogen from in-stream sources (Sanzone et al. 2003). Other animals, for which stream insects are a significant source of food, include lizards (Sabo and Power 2002) and even mammals (Santamarina 1993).

The proportion of emerged adults that do return is not known for any aquatic system with one notable exception. In an Arizona desert stream, Jackson and Fisher (1986) estimated aquatic insect return to be only 3% of the total insect biomass that emerged out of the water. This surprisingly low number prompted speculation that the numerous insectivorous birds observed in the riparian corridor were efficiently using the aquatic prey resource. It is not known whether aquatic insect populations in the wetter riparian climates of the Pacific Northwest exhibit similar patterns of low return.

Aquatic insects in the adult stage exhibit various behaviors for surviving during their time in the terrestrial environment. Some behaviors are believed to be adaptations to minimize vulnerability to predation. Mayflies, for example, forego feeding entirely as winged adults and live only a short time out of water, a few hours to a few days at most (Brittain 1982, Edmunds and Waltz 1996). Other adaptations associated with Ephemeroptera are daytime mating swarms which occur at synchronized times and locations to minimize extensive searching for mates and to numerically overwhelm any potential predators. Many species within the orders Trichoptera and Plecoptera have been shown to emerge at night and actively search for mates when light levels are low (Hynes 1976, Jackson and Resh 1991). While this adaptation helps to avoid daylight visual predators such as birds, it does not protect against echo-locating bats, or spiders, who are active both day and night (Gertsch 1949). Environmental factors other than predation - such as extreme high daytime temperature ( $> 35^{\circ} \text{C}$ ), which can cause desiccating conditions - may be another

reason for the high incidence of nocturnal activity for aquatic insects adults (Jackson 1988).

The theory that patterns of diel periodicity exhibited by adult aquatic insects are a response to riparian predation pressure has never been tested. Edmunds and Edmunds (1980) noted the almost total absence of adult mayflies in sweep net samples along rivers in Malaysia during daytime, despite their high abundance and diversity in the streams. They hypothesized that in response to heavy predation by daytime visual predators, mayflies had switched to a predominantly nocturnal adult life stage out of the water. At higher latitudes, where aquatic insects are mostly observed during the day, daytime predation pressure may not be strong enough to produce a behavioral switch to a more nocturnal activity pattern. It is also presumed that cold nighttime temperatures inhibit proper development in the adult stage. Since our study involved a mid-latitude stream insect community with both diurnally and nocturnally active species it was not clear which pattern would exhibit higher return for aquatic insects in the adult stage.

The longer an insect lives out of water, the more it is exposed to terrestrial predators and adverse climate conditions. Mayflies generally live for a very short time as adults and, we suspect, would have the highest proportion of returning individuals. Both caddisflies and many stoneflies can live much longer out of the water than mayflies, but for these groups, longevity is inversely dependent on the reproductive maturity at time of emergence. Adults of taxa emerging with fully formed eggs and sperm spend much less time out of water than those required to feed and develop their

eggs prior to mating (Zwick 1990, Wiggins 1996). Many spring-emergent limnephilid caddisflies from ephemeral water bodies are known to diapause as adults for several months before the fall rains allow them to return and oviposit their eggs in the water. Both short and long adult stages convey some advantage, but we do not know which strategy translates into higher proportions of returning adults to the stream.

The length of a species' emergence period might also have an impact on return proportion. The timing and location of emergence events, mating swarms, and oviposition flights may be fairly predictable from year to year. Though this predictability may vary between species, it is an important adaptation for finding mates and reducing exposure to predation (Edmunds and Edmunds 1980). However, predators such as birds and bats can take advantage of these predictable events by synchronizing foraging activity with the onset of emergence peaks (Gray 1993, Hayes 1997, Smith et al. 1998). Greater use of a prey resource may occur when it is more predictable for longer periods. Some populations of stream insects exhibit pulsed and synchronized emergence behavior where the entire event takes place in a few weeks. Others are spread over several months, with fewer individuals in the adult stage out of the water at any given time. As with adult-stage longevity, it is not clear whether the advantages gained from either strategy can be detected by measuring how many emerged adults make it back to the stream to oviposit.

The primary goal of this study was to determine the proportion of emerging EPT taxa that return to the stream - and consequently do not enter the terrestrial food web - along a 4<sup>th</sup> order montane stream in Western Oregon. We also wanted to link

this return proportion to three aspects of adult stage life history: diel activity in the adult stage, length of emergence period, and the longevity of the adult stage. We examined these activities during the summer of 2001 (22 June through 20 September).

Information on basic life histories of adult aquatic insects at the order, family, and species level have been compiled for many taxa in the Pacific Northwest, but not much is known about their behavior in terms of diel periodicity. Likewise, the relationship between an EPT taxon's diel activity and the number of returning adults to the stream is not known. Though diel periodicity appears to be a species-specific trait (Friesen, et al. 1980, Jackson and Resh 1991), we also considered broader levels of taxonomic resolution in our evaluations. Both daytime predators, such as birds, and nighttime hunters, such as bats, are common at our study site, but whether their foraging has an impact or not on the proportion of day-active and night-active adult aquatic insects cannot be surmised. Given this uncertainty, our investigation focused on whether day-active or night-active taxa are more successful at completing the adult stage and returning to the stream.

Similarly, we wanted to examine whether species with shorter or longer emergence periods and adult stages exhibited higher return numbers. Species with longer adult stages, such as many caddisflies, are exposed for longer periods to mortality factors such as predation, and we hypothesized that fewer individuals will return to the stream than the short-lived mayflies. Likewise, we speculated that species with emergence events of short, relatively pulsed, and synchronized duration would have more individuals returning than those with longer, more sustained

emergence periods. We theorize that predators focus their efforts on more long-term, predictable food sources.

During the course of the study period we counted the number of two common riparian insectivore guilds found in our study reach, birds and spiders, and observed changes in their densities over time. Our intention was to see if changes in the summer densities of these predators would be reflected in changes in aquatic insect prey abundances during the same period. If there is significant insect predation by these groups at our study site, then lower numbers of returning EPT adults might be associated with higher densities of birds and spiders.

## Site Description

Our study site was a 100 meter segment of Lookout Creek in the H. J. Andrews Experimental Forest in the western Cascade Mountains of Oregon (44.2 north latitude and 122.2 west longitude). At our site, Lookout Creek is a 4<sup>th</sup> order stream with a 1% slope. Stream width ranged from 6 m to 13.5 m with an average width of 10 m during summer base flows. The stream segment was an equal mix of pools, riffles, and glides; cobbles and boulders were the dominant substrates. The uppermost 30 meters consisted of two separate channels flowing around a cobble bar and was open to direct sunlight. Stream discharge measured at a gauge about 4 km downstream was 0.85 m<sup>3</sup>/s on 28 June 2001 and again on 13 July 2001, and declined steadily to a low of 0.21 m<sup>3</sup>/s at the conclusion of our field work on 20 September 2001. Discharge at our study site was approximately 20% less, based on flow measurements done at our site on 2 July 2001 and 11 September 2001. The riparian corridor of our study site was dominated by old growth Douglas-fir (*Pseudotsuga menziesii*) and western red-cedar (*Thuja plicata*). Understory trees included big-leaf maple (*Acer macrophyllum*), vine maple (*Acer circinatum*), and red alder (*Alnus rubra*). Shading of the channel by riparian vegetation in our study reach was substantial, especially in the downstream half, due to overhanging red alder and many conifers > 40 meters in height. Stream flow was from east to west.

## Methods

### Trap descriptions

Two types of in-stream traps were used to collect insects during two life stages: emergence traps, facing downward over the stream, collected freshly emerged adult macroinvertebrates, while upward-facing pan traps intercepted aquatic insects on their oviposition return flight to the stream as well as any terrestrial organisms that fell into the water. Our floating emergence traps (mesh size = 1mm) covered 0.25 m<sup>2</sup> of stream bottom. A plastic dish of unscented soapy water was suspended near the top of the trap from which the insects were collected. Pan traps consisted of two clear plastic containers of 15 cm depth held in place by a laundry basket and placed in-stream. They were filled with soapy water to about the water level of the stream. Surface area for each pan trap was 0.19 m<sup>2</sup>.

In addition, four hanging sticky traps were suspended from riparian vegetation to measure insect flight activity. Sticky traps consisted of a one meter square PVC frame with clear, plastic film stretched tightly across it. Before each sampling period, a portion of the center of the film was thinly coated on one side with Tanglefoot® adhesive, which remained relatively transparent after application.

### Sampling protocol:

Continuous emergence and pan trap sampling began on 6-25- 2001 and ended on 9-20-2001. We used ten of each trap type and placement in the stream was

random, relocating every two weeks. Traps were set for two 72-hour sampling periods each week; they were emptied and reset starting at 1700 hours each time. Once a week two concurrent 12-hour diel periods were established. Traps were set to collect a night/crepuscular sample starting at 1700 hours and ending at 0500 hours the next morning. The day sample began immediately after, starting at 0500 and ending at 1700. We collected a total of ten 12-hour day and ten 12-hour night diel samples. All samples from each type of trap were emptied into a 250 $\mu$ m mesh sieve, and the insects were preserved in 75 % ethanol.

Sticky traps were hung within three meters from the stream bank and no higher than two meters above the channel, sticky-side facing the stream. Two traps each were hung within 20 meters upstream and downstream from our study reach. Placement selection of these traps was not random, but was chosen to increase the number of insects caught and for efficiency in servicing. Flying insects adhered to the surface of the plastic film were counted visually with a 16X magnifying glass and identified to order after each 12-hour diel sampling period (0600 – 1800 = day; 1800 – 0600 = night).

#### Processing of samples:

Samples were first sorted into their respective orders; families of Ephemeroptera, Plecoptera, and Trichoptera were identified to determine which groups were most abundant. Target species were chosen based on high representation, the ease with which they could be identified to this taxonomic level, and the

availability of adult species keys for both males and females. Many of the aquatic insects at the H.J. Andrews Experimental Forest have been previously described (Parsons et al. 1991), and we used accounts of the emergence phenologies for Trichoptera (Anderson et al. 1984) and Ephemeroptera (Harper et al. 1995) species in Mack Creek, the major tributary to Lookout Creek a few miles above the study reach for verifying relative dominance among our taxa.

Calculating return proportion and diel activity:

We calculated return proportion for a given taxa as follows:

$$P_i\{\text{return}\} = R_i / E_i$$

where

$R_i$  = number of individuals /  $\text{m}^2$  / 24 hours in taxonomic group  $i$  caught in pan traps

$E_i$  = number of individuals /  $\text{m}^2$  / 24 hours in taxonomic group  $i$  caught in emergence traps

The passive nature of our measure of diel activity,  $P_i\{\text{night}\}$ , was simply the proportion of individuals of each taxon caught during the night 12-hour periods over the total number of individuals of that taxon caught in all day and night 12-hour periods, in both pan and emergence traps. Thus, a  $P_i\{\text{night}\} > 0.50$  was considered to be primarily nocturnal. As a hypothetical case, if we caught 100 individuals of taxon A from our diel sampling emergence and pan traps, of which 64 were from 12-hour night samples,  $P_A\{\text{night}\} = 0.64$ .

### Calculating adult longevity and emergence period:

We estimated adult longevity by creating timeline curves of emergence and return abundances for each species under scrutiny. Emergence and return abundance for a sample date was recorded as the number of individuals caught in either emergence or pan traps standardized for a 24-hour period and for a stream area of 1 m<sup>2</sup>. The time lag between the onset of emergence and the onset of return provided our primary estimate of adult longevity, measured in weeks. We also used the time lag between the last date of emergence and last date of return, or the peaks of each curve as secondary estimates for validation. When only the peaks or the end dates of each curve were captured during our field season, we used the timelag between the peaks as our primary estimate and the end dates for corroboration. When these methods produced two different estimates of adult longevity we reported the primary estimate and used it in further analysis. In some cases, especially for the mayflies, the temporal scale of our sampling schedule was not fine enough to detect a time lag between emergence and return. In these instances, we resorted to published accounts of adult longevity estimates for these or closely related species.

We used linear regression to evaluate any relationships between diel behavior, adult longevity and emergence period length with return proportion. The slope of the line indicated how well these species level characteristics could explain any observed differences in return success.

### Bird census:

Insectivorous birds were counted by visual binocular sightings for a 30 minute period between 0700 and 0800 one to two times a week, and within 24 hours of insect sampling. We flagged six 50 x 50 meter plots within the floodplain of the stream, three on either side immediately adjacent to the study reach. Plots were chosen at random the previous day with the toss of a die. After arriving in a plot, we waited for five minutes before the start of a census to allow birds disturbed by our approach into the area to return. Only known insectivores and only those within the 50 m x 50m plot were included. Omnivores such as the Stellar's jay (*Cyanocitta stelleri*) were included when they were observed foraging on insects.

### Spider census:

Spiders were censused by aggregating counts from three techniques from 2 August 2001 to 20 September 2001. Arboreal spiders on riparian vegetation were collected on large trays after bush-beating shrubs and branches overhanging the stream for five seconds, repeated five times. In addition, we counted ground-dwelling spiders by turning over 20 randomly chosen rocks on a cobble bar within the study reach, and counted active webs within a corridor 25 meters long, 3 meters wide, and 3 meters high running perpendicular from the edge of the stream. Counts were made concurrently once a week during midday and the results from all three methods were aggregated into an index score estimating relative spider densities. We also tracked the abundances of spiders that had unintentionally entered or fallen into our

emergence and pan traps. We considered their numbers in these traps as an indirect measure of riparian spider densities during the sampling period. We assessed the strength of the association between the number of spiders and emerging aquatic insects using linear regression.

## Results

Among EPT taxa, Trichoptera were the most numerous taxon in our emergence, pan, and sticky trap samples; four times as many Trichoptera individuals were caught as Ephemeroptera, and over ten times as many as Plecoptera (Fig. 1; Table 1). Of the 11 families of Trichoptera collected, Glossosomatidae, Philopotamidae, Hydropsychidae, and Rhyacophilidae were most common. The most abundant Ephemeroptera family was Baetidae, followed by Leptophlebiidae. The most common Plecoptera families found in our study reach were Chloroperlidae and Leuctridae. For our sample period, peak emergence and return for all orders occurred in the early summer, from the last week of June (Trichoptera and Plecoptera, Fig 1-A) to the second week of July (Ephemeroptera, Fig. 1-A).

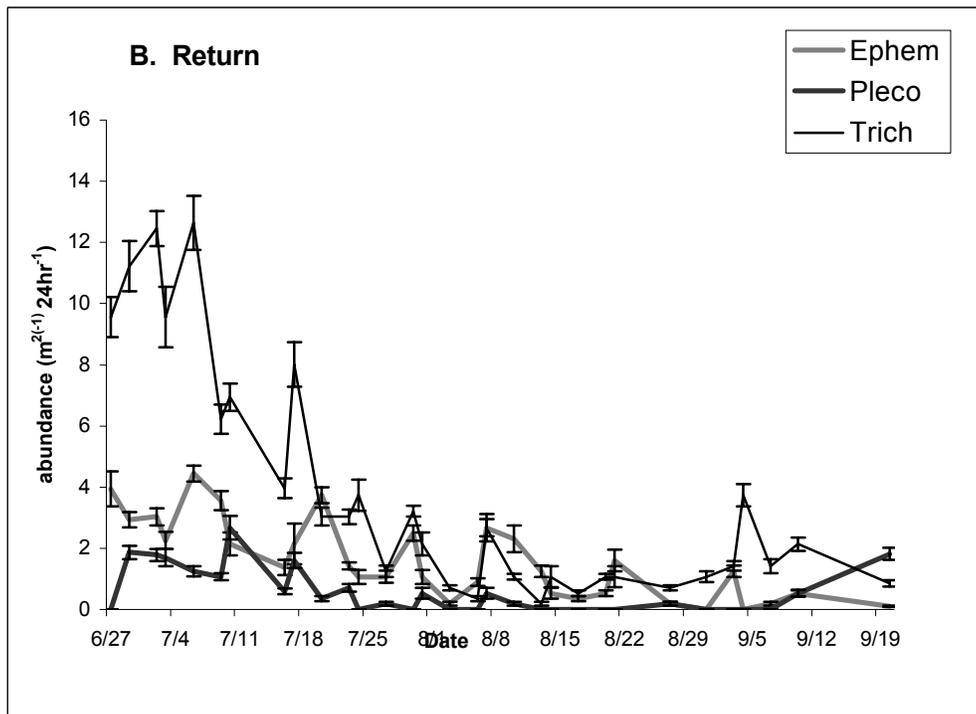
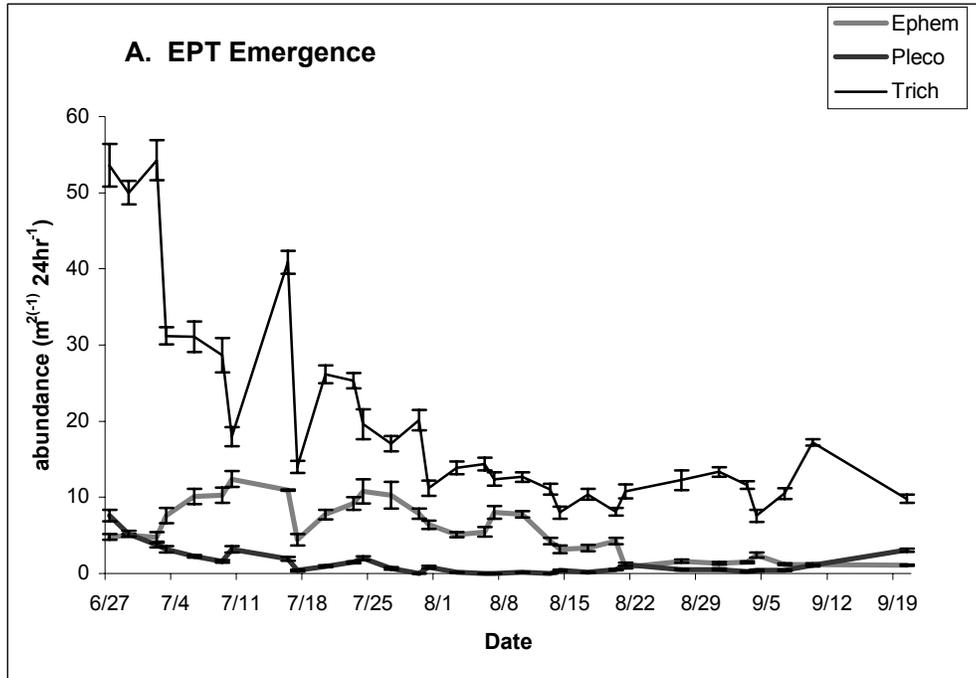
Table 1. Summary of EPT taxa collected at study site with P{return}, P{night}, total numbers in all samples (N) and total numbers in diel samples (N diel samples). Estimates and numbers for orders, families and genus are based on all individuals collected in each taxonomic category.

Order	Family	Species	P(return)	N	P(night)	N diel samples
<b>Trichoptera</b>			<b>0.18</b>	<b>4423</b>	<b>0.674</b>	<b>537</b>
	Glossosomatidae	all	0.07	1557	0.63	145
		Agapetus occidentis	0.17	113	0.29	7
		Glossosoma penitum	0.07	1378	0.65	138
	Philopotamidae	all	0.14	1218	0.84	154
		Dolophilodes dorcus	0.14	1124	0.84	154
	Lepidostomatidae	all	0.11	198	0.92	24
		Lepidostoma roafi	0.13	65	0.88	7
		Lepidostoma cascadense	0.06	67	0.91	11
		Lepidostoma unicolor	0.15	57	1.00	5
	Polycentropodidae	all	0.23	83	0.93	15
		Plectrocnemia variegatus	0.23	82	0.93	15

Table 1 (Continued)

Order	Family	Species	P(return)	N	P(night)	N diel sampling
	Hydropsychidae	all	0.30	701	0.54	128
	Rhyacophilidae	all	0.41	529	0.59	66
	Brachycentridae	all	0.07	45	0.80	5
	Uenoidae	All	0.36	30	1.00	4
	Limnephilidae	All	0.29	22	na	1
	Hydroptilidae	All	> 1.0	32	na	1
	Phryganeidae	All	0.61	7	na	1
<b>Plecoptera</b>			<b>0.37</b>	<b>392</b>	<b>0.40</b>	<b>60</b>
	Chloroperlidae	All	0.23	158	0.47	34
		Alloperla delicata	0.13	31	0.20	5
		Suwallia spp	0.40	20	0.53	8
		Sweltsa borealis	0.31	22	0.17	6
		Sweltsa fraterna	0.28	63	0.36	14
	Perlodidae	All	1.00	41	0.50	8
		Chernokrilus misnomus	0.99	28	0.67	6
	Nemouridae	All	0.78	48	0.18	11
		Zapada frigida	0.50	23	0.20	11
	Leuctridae	na	0.37	116	0.00	1
		Despaxia augusta	0.40	114	0.00	1
	Perlidae	na	0.07	27	0.57	7
<b>Ephemeroptera</b>			<b>0.28</b>	<b>1241</b>	<b>0.62</b>	<b>184</b>
	Baetidae	na	0.09	627	0.64	109
		Dipheter hageni	0.15	156	0.27	41
		Baetis spp	0.07	458	0.86	59
	Leptophlebiidae	na	0.83	298	0.46	28
		Paraleptophlebia temporalis	0.85	122	0.23	13
		Paraleptophlebia gregalis	0.84	130	0.58	12
		Paraleptophlebia sculleni	0.76	44	?	0
	Heptageniidae	na	0.28	158	0.60	30
		Epeorus (Iron) longimanus	0.24	82	0.86	14
		Epeorus (Iron) albertae	0.39	35	0.33	3
		Cinygmula reticulata	0.37	32	0.75	12
	Ephemerellidae	na	0.30	203	0.61	17
	Ameletidae	Ameletus spp	0.39	56	0.20	10

Fig. 1. Seasonal curves of emergence and return for EPT from all samples, summer 2001. Bars are standard error for 10 traps per sample date (Note: scale on y-axis not the same)



Estimates of  $P_{\text{return}}$ :

Plecoptera returned in the highest proportion (0.37) compared to Ephemeroptera (0.28) and Trichoptera (0.18) (Table 1). Return proportions of families and species within all three orders varied greatly. In the Trichoptera,  $P_{\text{return}}$  ranged from a low of 0.07 for the glossosomatid caddisflies to a high of  $>1.0$  in the family Hydroptilidae. The Plecoptera were similarly varied with a low of 0.07 for the perlid stoneflies, and a high of 1.00 for the Perlodidae. The range exhibited by Ephemeroptera families was only slightly narrower, 0.09 (Baetidae) to 0.83 (Leptophlebiidae).

$P_{\text{return}}$  among species of the same family were less variable than among families within an order, i.e. estimates of  $P_{\text{return}}$  among con-familial or even con-generic species were relatively close (Table 1). In all three *Paraleptophlebia* species, for example, we observed extremely high  $P_{\text{return}}$  (0.85, 0.84, and 0.76), while the three caddisfly species of *Lepidostoma* exhibited relatively low  $P_{\text{return}}$  (0.16, 0.13, and 0.06). The three observed species within the Heptageniidae were also similar in their  $P_{\text{return}}$  ranging from 0.24 to 0.39. The most variation for  $P_{\text{return}}$  within a family was exhibited by the four species of Chloroperlidae, with the proportion for *Alloperla delicata* (0.13) much lower than for the other, more closely related species (0.28-0.40).

### Estimates of $P_{\text{night}}$

At the order level, Trichoptera were most nocturnal with a  $P_{\text{night}}$  of 0.67, whereas Plecoptera were the least nocturnal with a  $P_{\text{night}}$  of 0.40. The diel patterns from the emergence and pan traps were also borne out by the hanging sticky traps (Fig. 2 A). However, Ephemeroptera showed a preference for night emergence and return ( $P_{\text{night}} = 0.62$ ) according to emergence and pan trap collections, but an affinity for day activity based on the hanging sticky traps ( $P_{\text{night}} = 0.35$ ) (Fig 2 A and B).

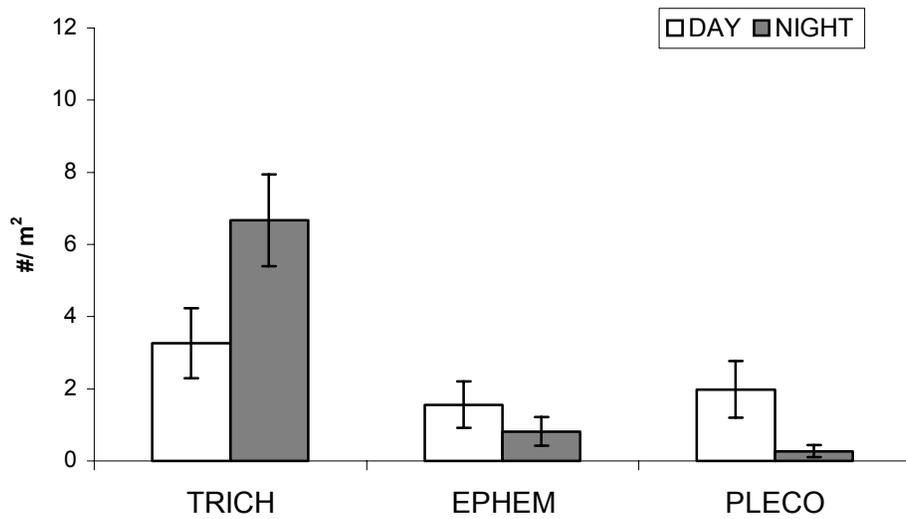
At finer levels of taxonomic resolution, the degree of nocturnal activity among taxa were highly variable (Table 1), suggesting that diel activity in the adult stage is a species-specific trait. For families across all three orders where numbers of collected individuals  $> 10$ , the range of  $P_{\text{night}}$  was between 0.18 and 0.93. All caddisfly families were predominantly nocturnal (range = 0.54 – 0.93); for Lepidostomatidae and Polycentropodidae  $P_{\text{night}}$  exceeded 0.90. Ephemeroptera had representatives of both day-active and night-active families. Ameletidae were distinctly day-active ( $P_{\text{night}} = 0.20$ ) and Leptophlebiidae tended slightly towards day-active ( $P_{\text{night}} = 0.46$ ). Other mayfly families tended towards night-active (0.60-0.64) but not to the same degree as caddisflies. Among the Plecoptera, only the Chloroperlidae ( $P_{\text{night}} = 0.47$ ) and the Nemouridae ( $P_{\text{night}} = 0.18$ ) were sufficiently numerous in our diel samples to provide us with adequate estimates.

At the species level, there was wide variation in diel activity patterns, even between species of the same family. For example, the two Glossosomatid caddisflies *Agapetus occidentis* and *Glossosoma penitum* showed remarkably different diel preferences with  $P_{\text{night}}$  of 0.29 and 0.65, respectively. However, congeneric species within the Trichoptera and Plecoptera tended to be more similar in their diel activity. All three *Lepidostoma* were predominantly caught in night traps, while both *Sweltsa* species preferred daytime for emerging and returning to and from the water.

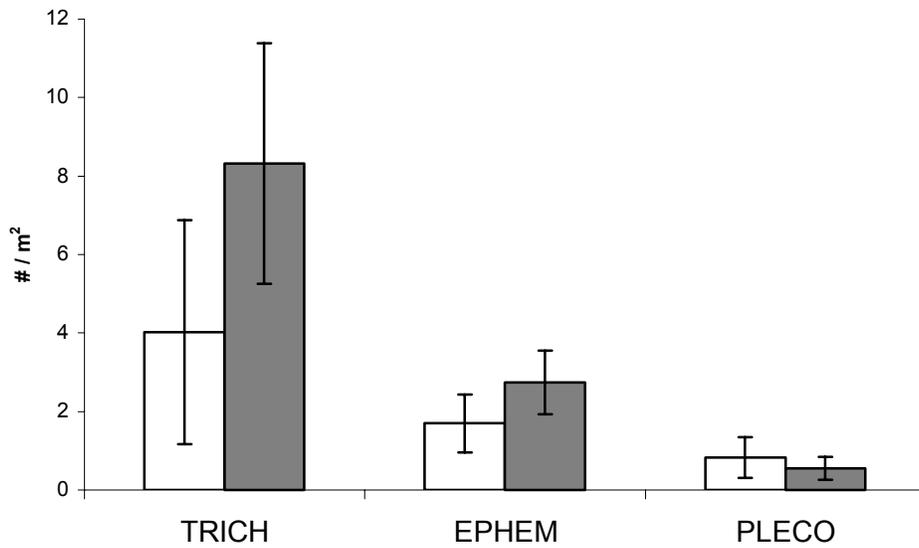
The two generic complexes we identified among the mayflies, *Paraleptophlebia* spp. and *Epeorus (Iron)* spp., both showed wide differences in their diel activity pattern; we qualify the latter estimate as we had only three individuals of *Epeorus albertae* in our diel emergence and pan traps. *Baetis* spp. emerging throughout the summer were much more frequent in night traps with a  $P_{\text{night}}$  of 0.86, while the other common baetid mayfly, *Dipheter hageni*, was more diurnal (0.27).

Fig 2 - A: Diel flight activity for Trichoptera, Ephemeroptera, and Plecoptera from hanging traps along stream bank. Numbers are per  $m^2$  per 12-hour sample period for all hanging sticky traps summed from seven sample dates between 7-17-01 to 9-4-01. B: Composition of diel samples from emergence and pan traps. Numbers are per  $m^2$  per 12-hour sample period summed from ten sample date between 6-27-01 to 9-4-01.

A



B



To examine whether return proportion was related to diel patterns of activity, we compared  $P\{\text{return}\}$  to  $P\{\text{night}\}$  at family and species level (Figs. 3 and 4). We detected a moderately weak negative trend between the level of nocturnal activity and the corresponding  $P\{\text{return}\}$  for families with at least 10 individuals caught in diel traps ( $R^2 = 0.42$ ,  $p < 0.02$ ; Fig. 3). At the species level, when we include species with at least seven individuals caught in diel traps, we observed a weaker negative trend ( $R^2 = 0.22$ ,  $p < 0.08$ ; Fig. 4). At both levels, caddisfly taxa are closely grouped at the top left of the scatter plot, reflecting their overall lower return proportion and propensity for nocturnal activity, while mayflies, scattered widely across the plot area, exhibited a wide range in diel activity and return proportion.

Fig 3. Relationship between return proportion and diel activity for EPT families. Only families with 10 or more representatives within the diel samples were used in this analysis.

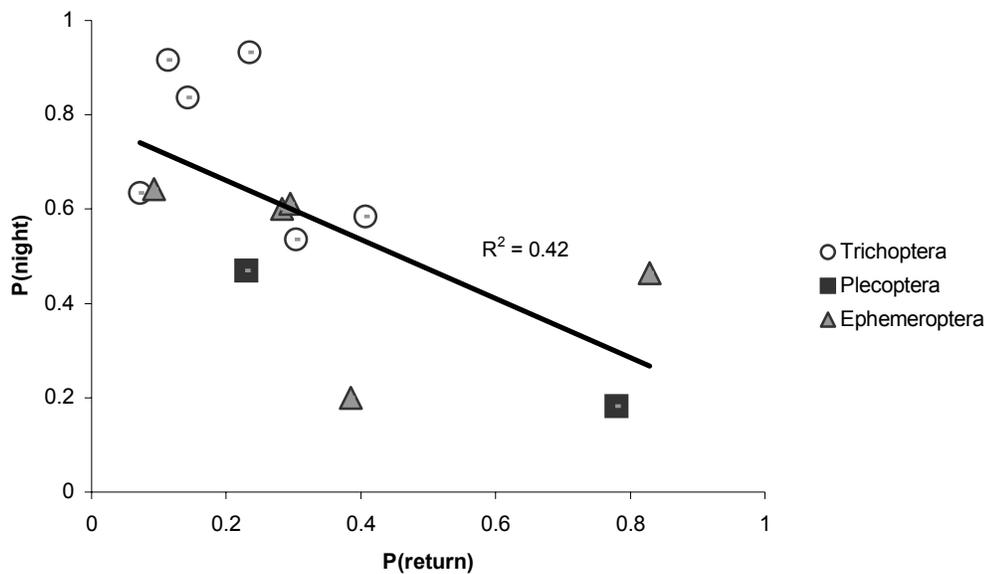
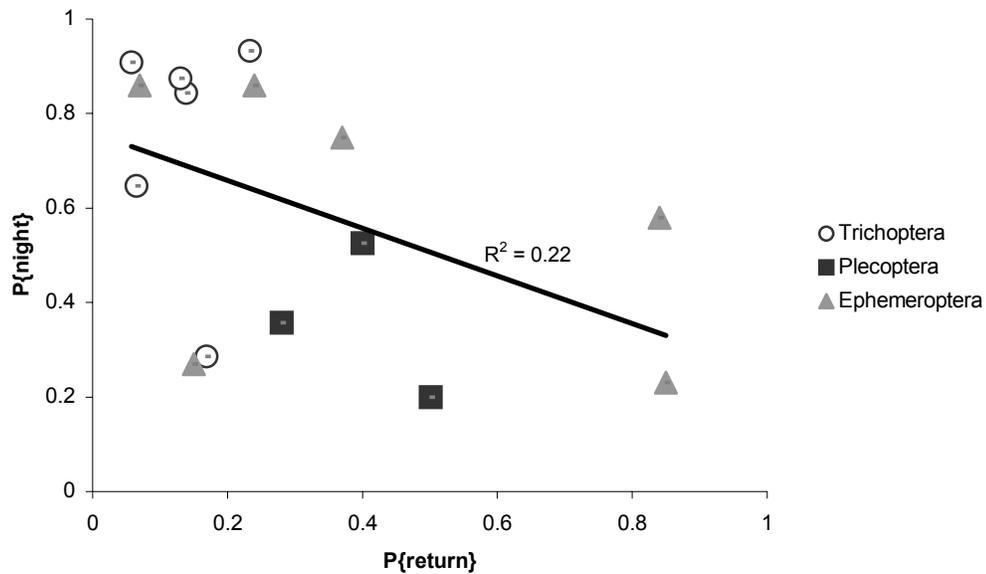


Fig 4. Relationship between return proportion and diel activity for EPT species. Species with at least 7 or more representatives in the diel samples were used in this analysis.

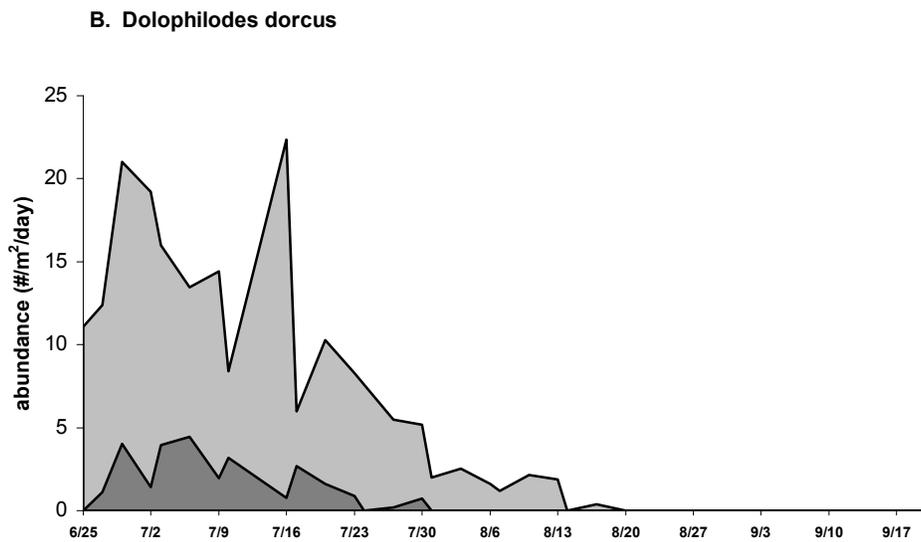
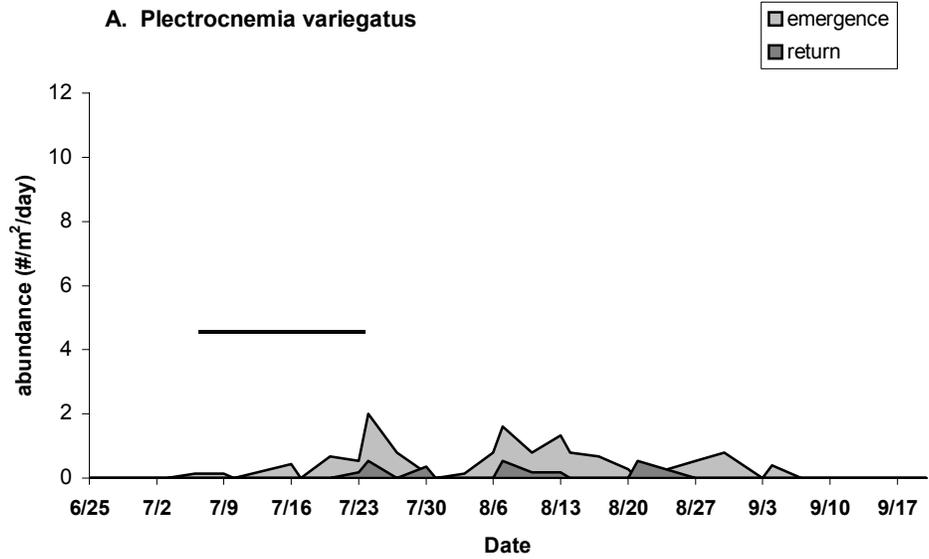


Length of emergence period:

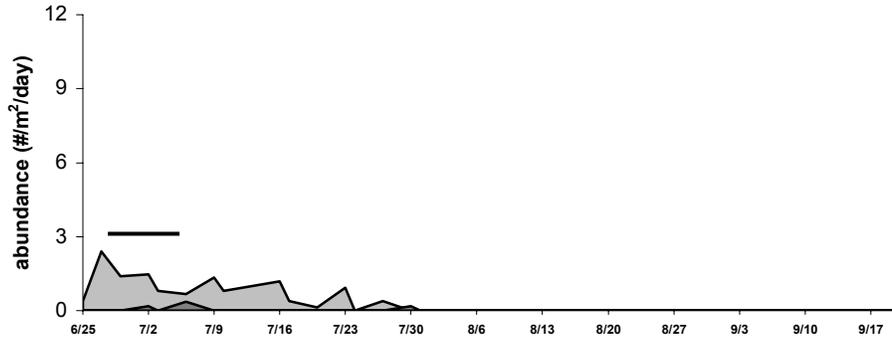
Stonefly species had the shortest mean emergence periods ( $\mu = 4.6$  weeks), while caddisflies had the longest ( $\mu = 7.7$  weeks) (Tables 2-4). The majority of species could be categorized into two groups - those with short (i.e. 3-6 weeks) and those with extended (i.e. 8-10 weeks) emergence periods. Most caddisflies (Fig. 5A-F) and the mayfly *E. (Iron) tongimanus* (Appendix, Fig. 3) had emergence periods of eight or more weeks, while all stonefly species (Fig. 7A-E) and all other mayfly species emerged in 3-6 weeks (Fig 6, A-C; Appendix Figs. 2, 4 – 6). The one caddisfly that fell into this shorter interval, *Lepidostoma unicolor*, was the second of three

*Lepidostoma* species emerging in temporal sequence (Fig. 5D). *Glossosoma penitum* showed a marked difference from other EPT taxa and did not conform to either group (Fig. 5F). Its emergence period extended beyond the 13-week field season and most likely has a starting date in early spring. Based on previous studies of this species (Anderson and Bourne 1974, Anderson et al. 1984) we conservatively estimated an emergence period length of 30 weeks. The relationship between length of emergence period and P{return} was negative ( $R^2 = 0.34$ , p-value < 0.02), i.e. species with shorter emergence periods tended to return back to the stream more successfully than those with extended emergence periods (Fig. 8).

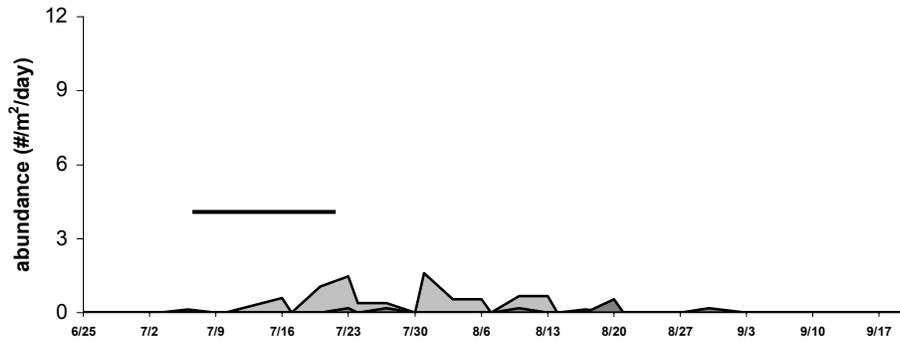
Figure 5, A-G: Emergence and return curves for Trichoptera species from 6-25-01 to 9-20-01. Line above curves are estimates of adult longevity.



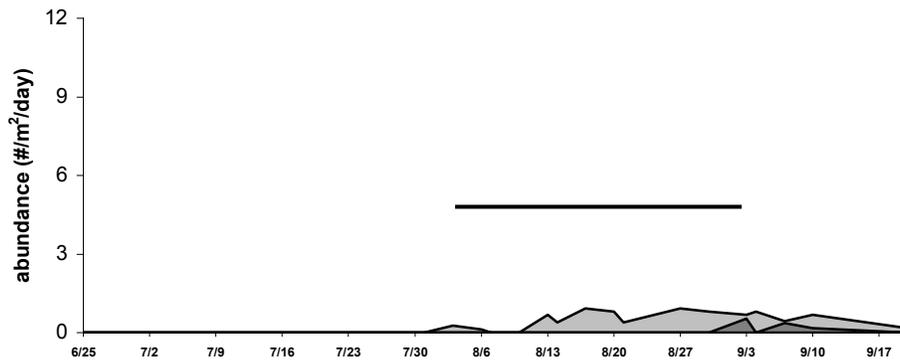
**C. *Lepidostoma cascadense***



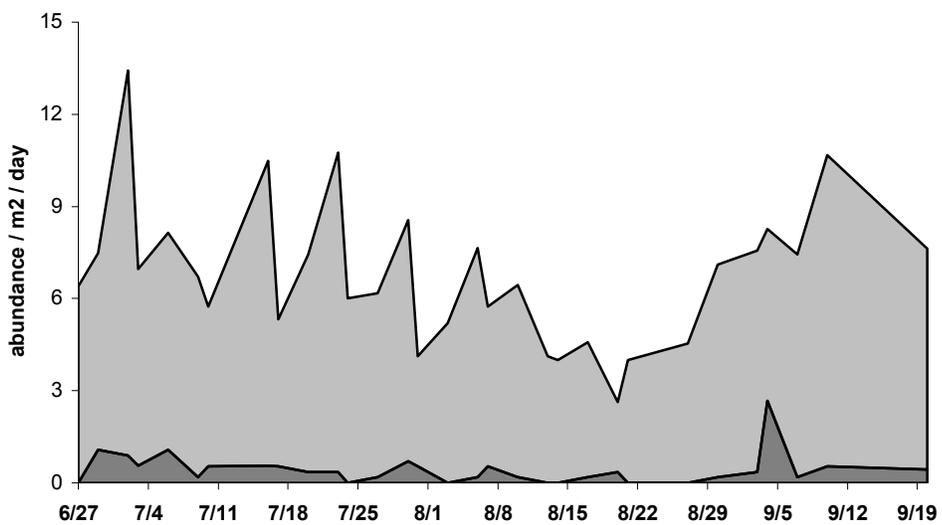
**D. *Lepidostoma unicolor***



**E. *Lepidostoma roafi***



**F. *Glossosoma penitum***



**G. *Agapetus occidentis***

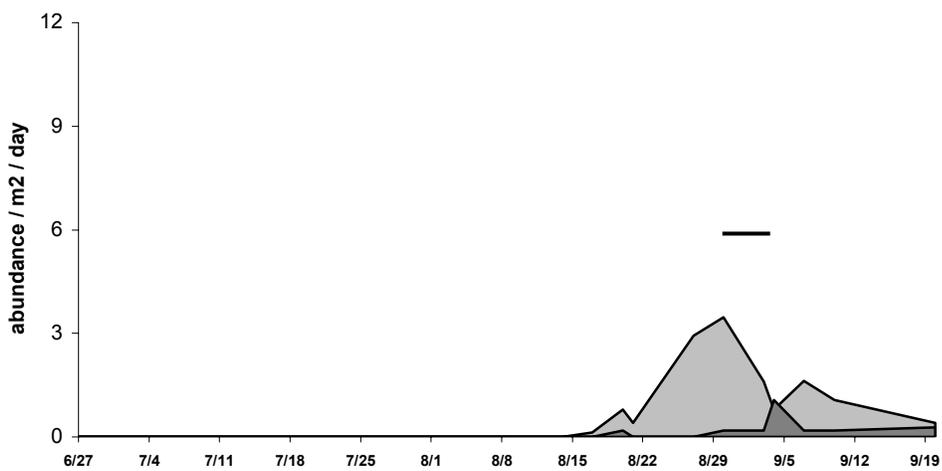
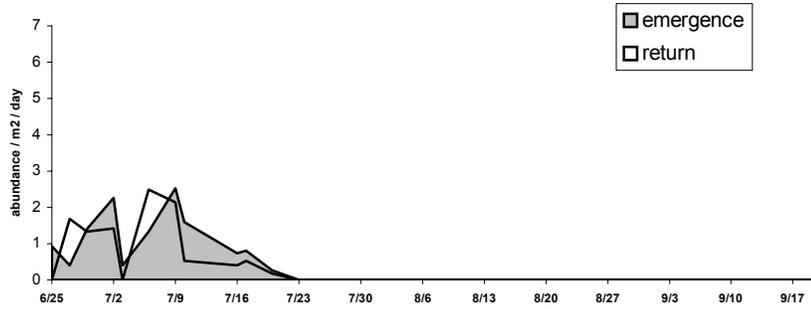
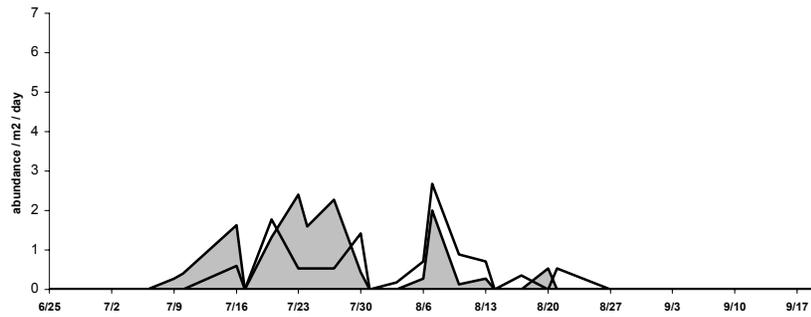


Fig. 6, A-C: Emergence and return curves for *Paraleptophlebia* species (Ephemeroptera) from 6-25-01 to 9-20-01

**A. *Paraleptophlebia temporalis***



**B. *Paraleptophlebia gregalis***



**C. *Paraleptophlebia sculleni***

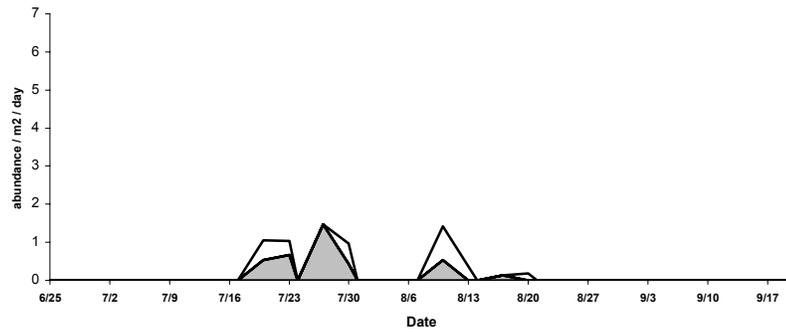
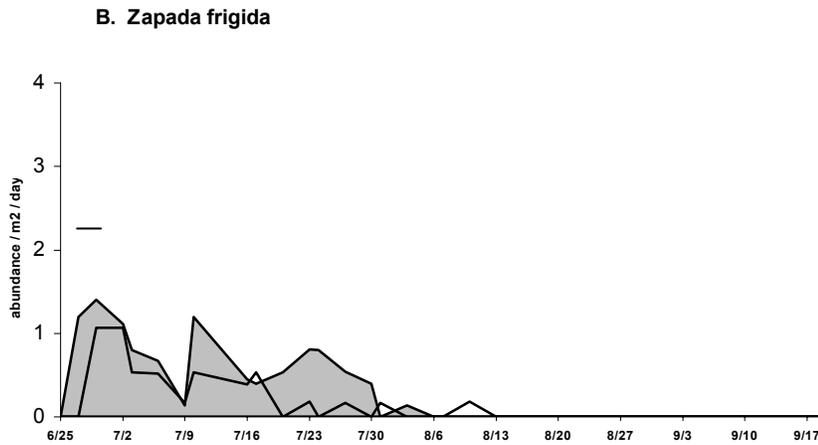
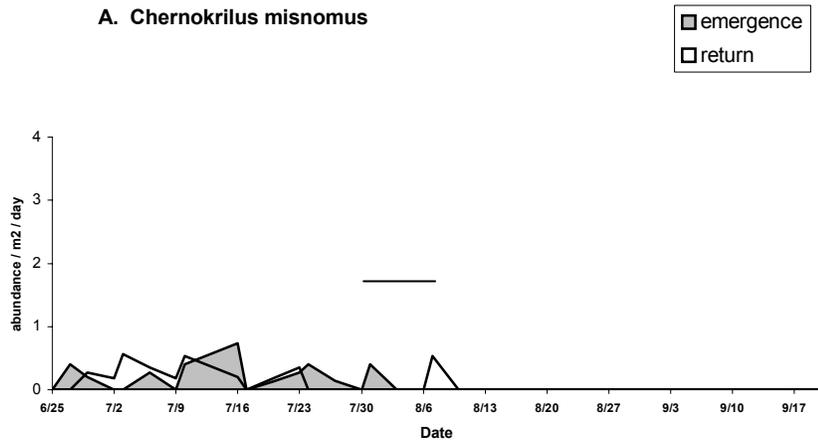
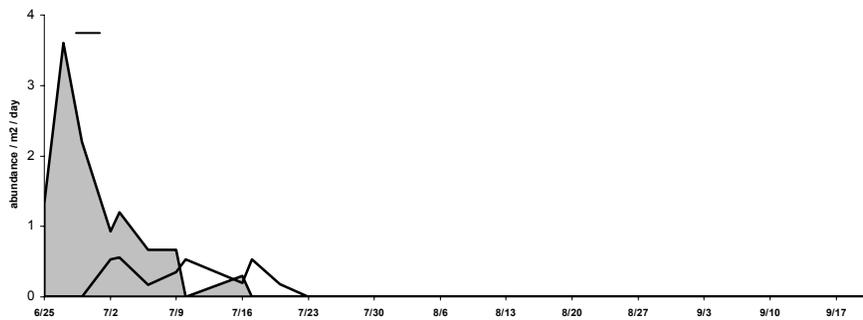


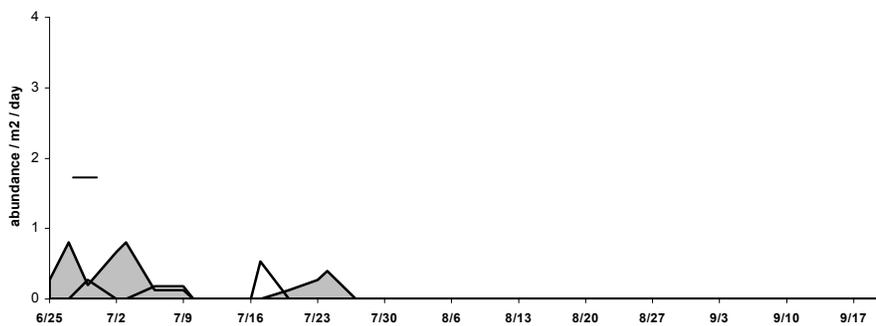
Fig 7, A-E: Emergence and return curves for Plecoptera species from 6-25-01 to 9-20-01.



**C. Sweltsa fraterna**



**D. Sweltsa borealis**



**E. Alloperla delicata**

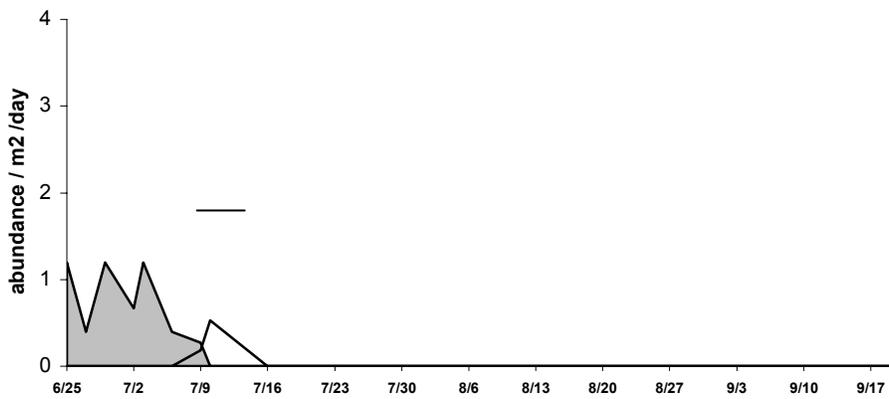
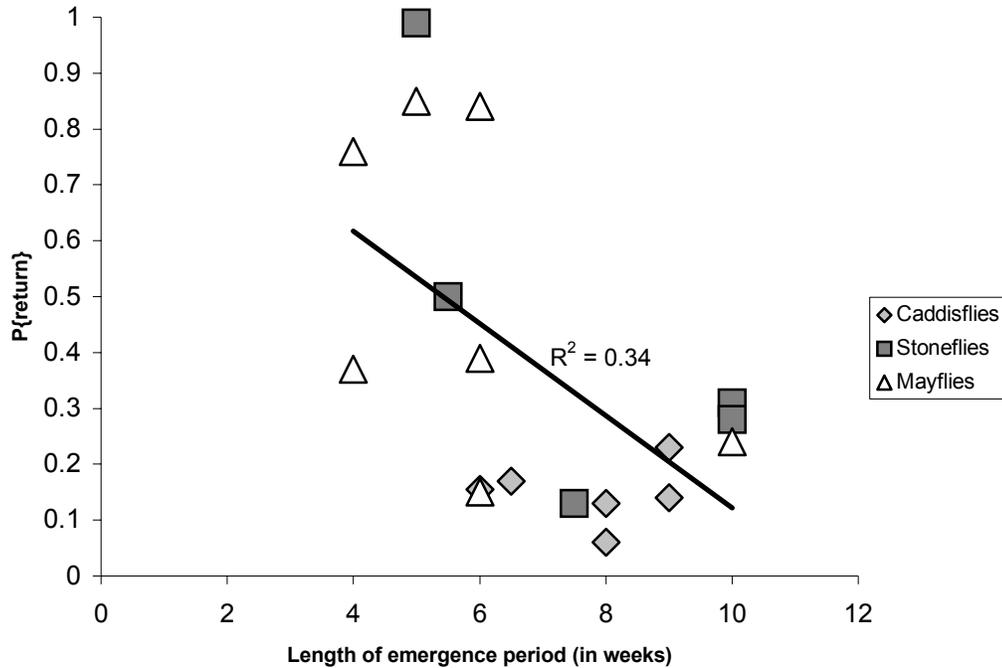


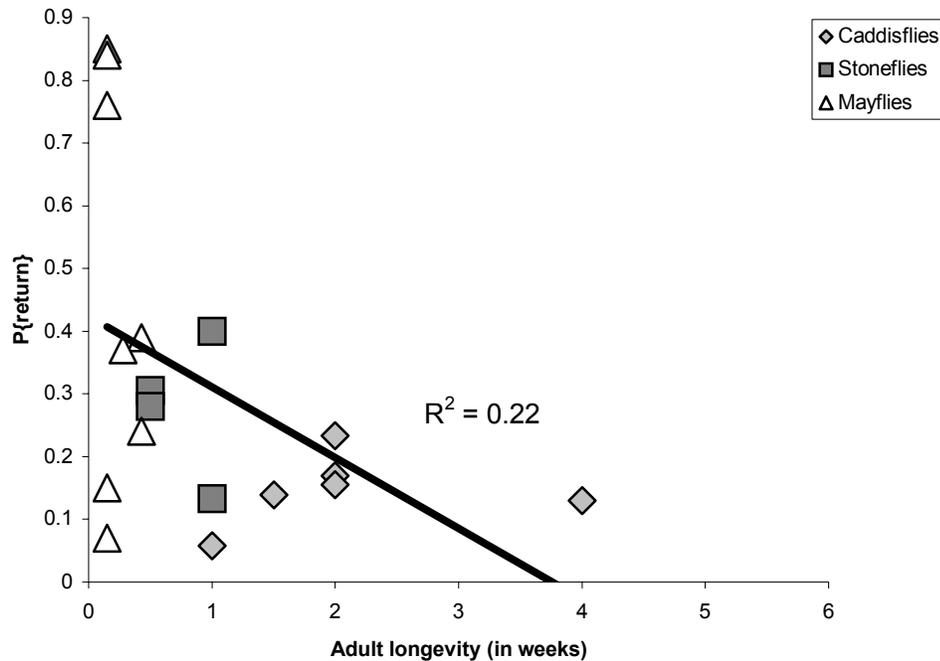
Fig. 8: Comparison of EPT emergence periods to return proportion.



#### Adult longevity:

Based partly on our seasonal abundance curves and partly on the scientific literature, we estimated adult stage longevity for 4 out of 7 species of stoneflies collected, 6 out of 7 caddisflies, and all 8 mayflies. As expected, caddisflies on average live the longest in the adult stage, followed by stoneflies and finally mayflies, which appear to spend a maximum of only a few days out of the water. The relationship between adult longevity and return proportion across all taxa is weakly negative ( $R^2 = 0.22$ ,  $p$ -value  $< 0.06$ ; Fig. 9), driven primarily by caddisflies. There is only slight evidence that longer-lived species return in fewer numbers to the stream than those with shorter adult life spans.

Fig 9: Adult longevity compared to return proportion for EPT taxa.



Estimates of Trichoptera adult longevity were extremely variable, from 0.6 to 4 weeks (Table 4). Adult caddisfly longevity estimates based on seasonal abundance curves generated from both emergence and return samples included those for *Dolophilodes dorcus* (Fig. 5-B), all three *Lepidostoma* species (Fig. 5-C, D, E), *Agapetus occidentis* (Fig. 5G) and *Plectrocnemia variegatus* (Fig. 5-A). We were able to capture the entire emergence event for *P. variegatus* within our field season, and longevity was estimated at approximately two weeks. *Dolophilodes dorcus* was very abundant in our samples, but the beginning of the emergence event was not captured during the field season. From previous work with emergence trapping on

Table 2: Ephemeroptera species, total numbers captured, return proportion, and estimates of adult longevity and emergence period compared at Lookout Creek, OR., with estimates from other sources.

Family	Species	P(return)	N	longevity (days)	Other estimates of adult longevity	Source (adult longevity)	length of emergence period, LEP (weeks)	Other estimates of LEP	Source (LEP)
Baetidae	Dipheter hageni	0.15	156		1, based on <i>Baetis spp</i>	Wallace and Anderson, 1996	6	4 to 6	Harper, et al. 1995
Baetidae	Baetis spp	0.07	458		1, based on <i>Baetis spp</i>	Wallace and Anderson, 1996			
Leptophlebiidae	Paraleptophlebia temporalis	0.85	122		1	Lehmkuhl and Anderson, 1971		5	Harper, et al. 1995
Leptophlebiidae	Paraleptophlebia gregalis	0.84	130		1, based on <i>P. temporalis</i>	Lehmkuhl and Anderson, 1971	6		this study
Leptophlebiidae	Paraleptophlebia sculleni	0.76	44		1, based on <i>P. temporalis</i>	Lehmkuhl and Anderson, 1971	4		this study
Heptageniidae	Epeorus (Iron) longimanus	0.24	82		3	Edmunds and Allen, 1964		10	Harper, et al. 1995
Heptageniidae	Epeorus (Iron) albertae	0.39	35		3, based on <i>E. longimanus</i>	Edmunds and Allen, 1964	6		Edmunds and Allen, 1964
Heptageniidae	Cinygmula reticulata	0.37	32		2	Lehmkuhl and Anderson, 1970		4	Harper, et al. 1995
all	All	0.28	1241						

Table 3: Plecoptera species, total numbers captured, return proportion, and estimates of adult longevity and emergence period at Lookout Creek, OR., compared with estimates from other sources.

Family	Species	P(return)	N	longevity (weeks)	Other estimates of adult longevity	Source (adult longevity)	length of emergence period, LEP (weeks)	Other estimates of LEP	Source (LEP)
Chloroperlidae	<i>Alloperla delicata</i>	0.13	31	1 <sup>3</sup>		this study		8	Kerst and Anderson, 1975
Chloroperlidae	<i>Suwallia</i> spp	0.40	20				3	6, <i>S. pallidula</i>	Kerst and Anderson, 1975
Chloroperlidae	<i>Sweltsa borealis</i>	0.31	22	0.5 <sup>1</sup>	2	Yoshimura et al., 2003		10	Kerst and Anderson, 1975
Chloroperlidae	<i>Sweltsa fraterna</i>	0.28	63	0.5 <sup>2,3</sup>	2	Yoshimura et al., 2003		10	Kerst and Anderson, 1975
Perlidae	<i>Chemokrilus misnomus</i>	0.99	28	1 <sup>1,3</sup>		this study	5		this study
Nemouridae	<i>Zapada frigida</i>	0.50	23	0.5 <sup>1,2</sup>	3-8, other Nemouridae	Zwick, 1990	6	14	Kerst and Anderson, 1975
Leuctridae	<i>Despaxia augusta</i>	0.40	114	1 <sup>1</sup>		this study		6.5	Richardson, 2001
all	all	0.37	392						

(<sup>1</sup> – time difference between start dates; <sup>2</sup> – time difference between peaks; <sup>3</sup> – time difference between end dates)

Table 4: Trichoptera species total numbers captured, return proportion, and estimates of adult longevity and emergence period at Lookout Creek, OR., compared to estimates from other sources.

Family	Species	P(return)	N	longevity (weeks)	Other estimates of adult longevity	Source (adult longevity)	length of emergence period (weeks)	Other estimates of LEP	Source
Glossosomatidae	<i>Agapetus occidentis</i>	0.17	113	0.6 <sup>1,2</sup>	few days ( <i>Agapetus fuscipes</i> )	Wallace and Anderson, 1996	6.5		this study
Glossosomatidae	<i>Glossosoma penitum</i>	0.07	1378					30	Anderson and Bourne, 1974
Philopotamidae	<i>Dolophilodes dorcus</i>	0.14	1124	1.5 <sup>1</sup>				9	Anderson et al. 1984
Lepidostomatidae	<i>Lepidostoma roafi</i>	0.13	65	4 <sup>1</sup>			8		this study
Lepidostomatidae	<i>Lepidostoma cascadense</i>	0.06	67	1 <sup>1</sup>				8	Anderson et al. 1984
Lepidostomatidae	<i>Lepidostoma unicolor</i>	0.15	57	2 <sup>1,3</sup>			6		this study
Polycentropodidae	<i>Plectrocnemia variegatus</i>	0.23	82	2.5 <sup>1</sup>			9		this study
<b>all</b>	<b>all</b>	<b>0.18</b>	<b>4423</b>						

(<sup>1</sup> – time difference between start dates; <sup>2</sup> – time difference between peaks; <sup>3</sup> – time difference between end dates).

Mack Creek, a 3<sup>rd</sup> order tributary of Lookout Creek (Anderson et al. 1984), we estimated the emergence period for this species to have started around the third week of June or one week before our field season began. Based on this estimate we set a length of emergence period at 9 weeks and an adult longevity of one week. Heavy rains on July 13<sup>th</sup> may account for the second spike on the emergence curve.

The three *Lepidostoma* species exhibited a clear sequencing of emergence phenology, with *L. cascadense* emerging first, followed by *L. unicolor* and finally *L. roafi* (Fig. 5-C, D, E). Our estimates of adult longevity among the *Lepidostoma* varied considerably. *L. cascadense* had the shortest adult stage, about one week, followed by *L. unicolor* with an adult stage lasting about 2 weeks, and finally *L. roafi* with the longest adult stage (4 weeks). All three species had low P{return}.

We could not establish an estimate of adult longevity for *Glossosoma penitum* (Fig. 5-F) because of its extremely long emergence period, which exceeded the length of our field study. *Glossosoma penitum* was the most numerous species among EPT taxa and was captured throughout the field season in high numbers. Because of its low P{return} of 0.07 and consistently high numbers, *G. penitum* probably contributed the most to riparian food webs during our field season. In comparison, the other glossosomatid caddisfly, *Agapetus occidentis*, exhibited a relatively discrete period of activity in the adult stage, from mid-August through the end of the field season. We based our estimate of adult longevity on the difference in time between peak emergence and return, about 4 days.

The stoneflies varied in how long they lived in the adult stage, from a few days in the *Sweltsa* species, to 1-2 weeks for *Chernokrilus misnomus* and *Alloperla delicata* (Fig. 7-A to E; Table 3). Overall numbers of stoneflies were much lower than for other groups and the presence of some species in our samples were sporadic. Some of our estimates are therefore very tentative. *Zapada frigida* had a shorter adult stage than expected (less than one week) based on published data of other species within the family Nemouridae. Similarly, our estimates of adult longevity for *Sweltsa borealis* and *S. fraterna* (both less than one week) were shorter than other published accounts.

Because mayflies live for very short periods after emergence, temporal resolution of our sampling schedule was not sufficiently fine to detect adult longevity (e.g. *Paraleptophlebia* spp., Fig. 6-A to C). Return curves tended to mirror emergences, indicating a short adult life between the time of emergence and oviposition. Estimates for the species at our study site were gleaned from the existing literature and ranged from 1 day in the two Baetidae and the three *Paraleptophlebia* species to 3 days in *Epeorus (Iron) longimanus* (Table 2). We estimated *Epeorus (Iron) albertae* adult longevity to be similar to its congeneric (3 days), while *Cinygmula reticulata* reportedly lives 2 days outside of the water.

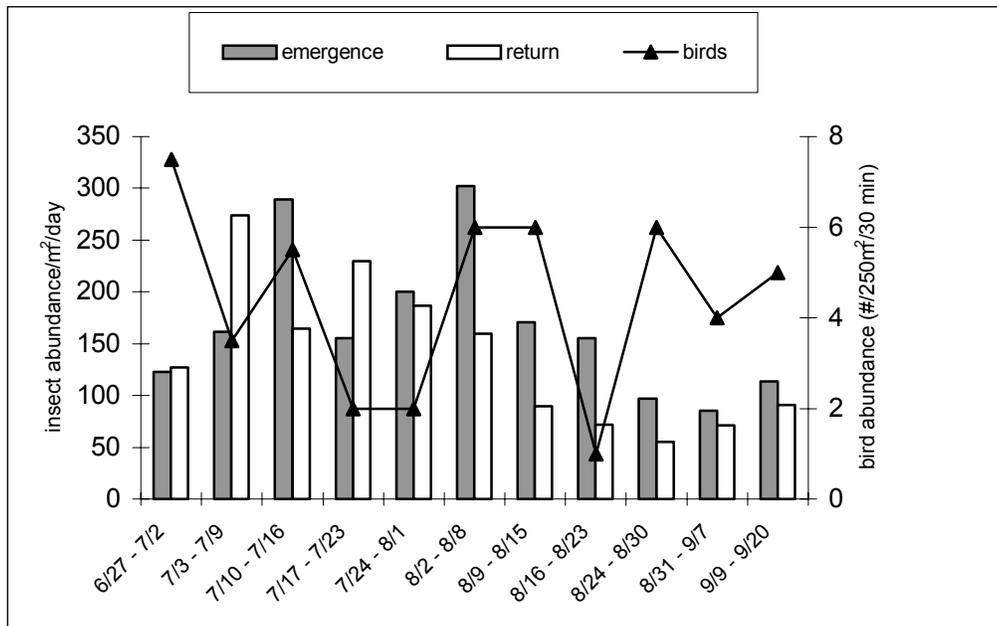
To evaluate the effect of all three life history parameters (diel behavior, length of emergence period, adult stage longevity, order designation) simultaneously, we used multiple regression, with P{return} as response variable. In this more generalized approach, there was no evidence that any combination of the explanatory

variables significantly affected return proportion (F-stat = 1.309; 6 and 10 df; p-value = 0.34).

Predators:

Bird densities within our study section of the stream were low throughout the summer, ranging from 1 – 8 birds per 50m x 50m plot area during the 30-minute count period. Fifteen species were observed in our counts; *Poecile rufescens* (chestnut-backed chickadee), *Troglodytes troglodytes* (winter wren), and *Empidonax hammondii* (Hammond’s flycatcher) were the most common. Bird densities do not appear to respond to total prey densities as measured from both emergence and pan trap samples (Fig. 10).

Fig 10. Riparian insectivorous bird densities, total aquatic insect emergence and total insect return (i.e. EPT + other arthropod taxa) over the summer. Counts of both insects and birds were made within 24 hours of each other.



Many spiders were found in both emergence and pan trap samples, either from falling onto the traps from overhanging vegetation or by ballooning (Fig. 11, 12-A). Over the summer, riparian spider density based on in-stream trap samples peaked approximately two weeks earlier than the direct counts (Fig. 12-B), but show a similar gradual increase until August, followed by a greater decline into September. One discrepancy to this trend occurred with our counts of spiders found among the cobbles and boulders. In this case, numbers increased steadily through August and September (Fig. 12-B, most likely due to the receding stream discharge, which exposed more suitable habitat for ground-dwelling spiders, primarily Lycosidae (wolf spiders).

Fig 11. Riparian spider densities in traps, total aquatic insect emergence and return (i.e. EPT + other arthropod taxa), summer 2001.

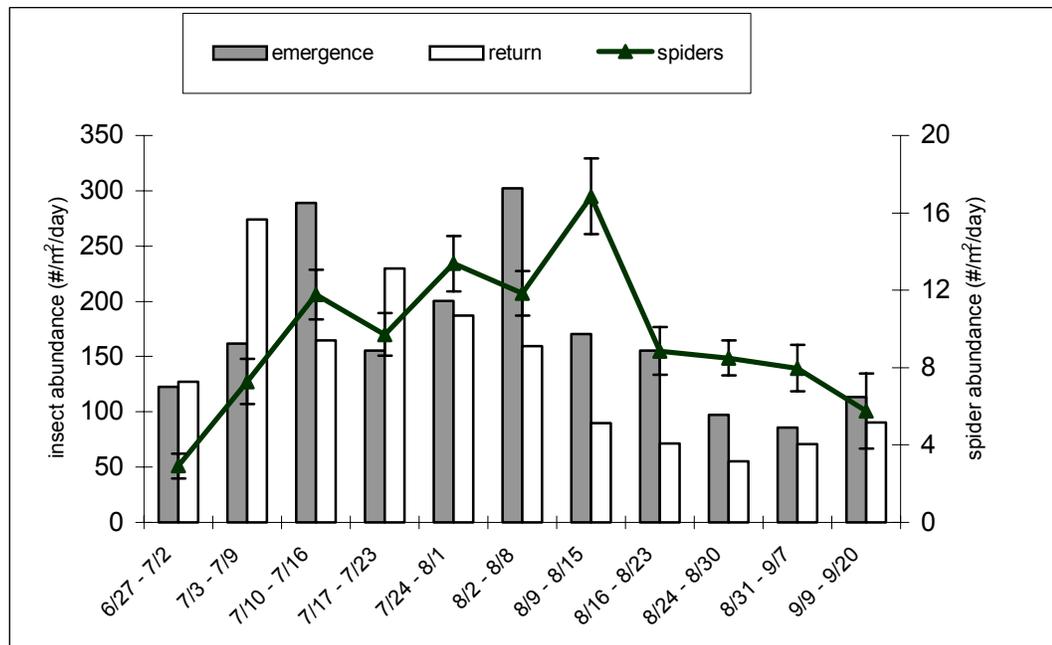
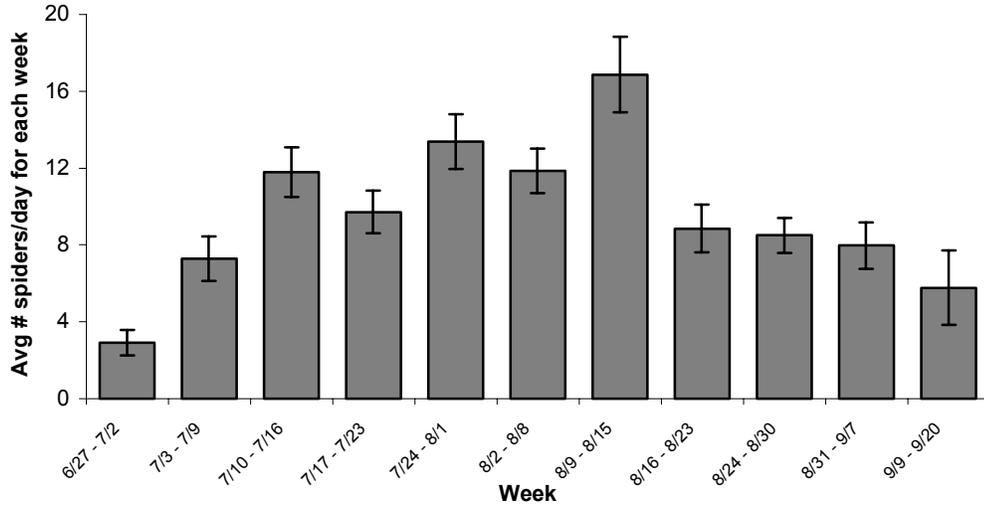
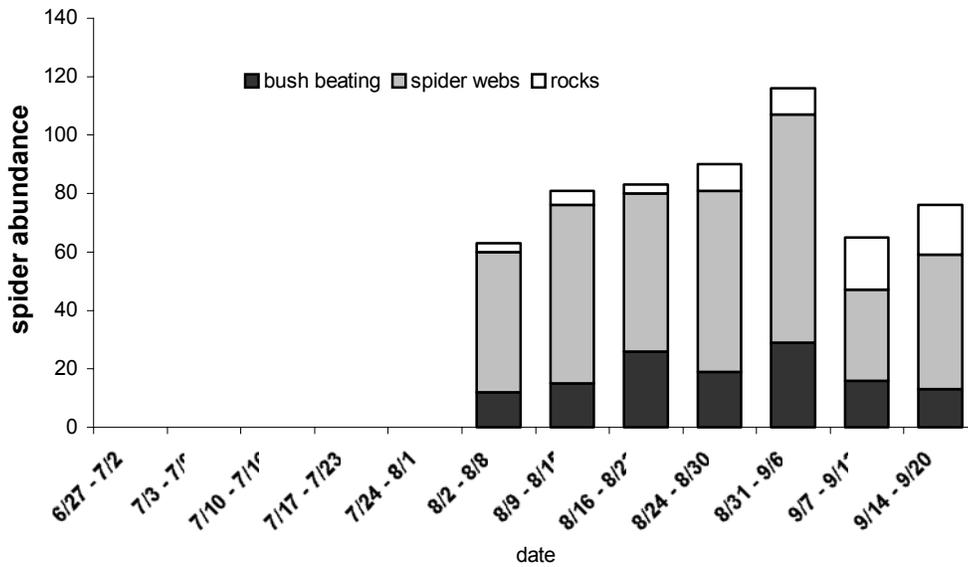


Fig 12. Riparian spider counts: Figure 12-A: spiders incidentally caught in emergence and pan traps with standard error bars. 12-B: aggregate results from direct spider counts.

**A. Spiders caught in traps, 6/27/01 to 9/20/01**



**B. Spider abundance from direct riparian counts**



Overall spider abundance along the stream from direct counts peaked in the fourth week of August. The majority of the spiders we counted were web-weaving spiders, e.g. *Tetragnatha spp.* We observed between 0.14 – 0.35 active webs /m<sup>3</sup> in the riparian vegetation. Spiders from in-stream traps appear to track aquatic insect emergence well (Fig. 11), and the relationship between spiders and total emerging aquatic insects was statistically significant ( $R^2 = 0.29$ , p-value < 0.04).

## Discussion

The most significant aspects of our results were the patterns of return proportion at different taxonomic levels. Return proportion within each of the orders varied considerably from species to species, but at each higher taxonomic level, the range of our estimates of return proportion narrowed. The similarity of our P {return} estimates in closely related groups is striking given the wide range of these estimates overall. Although this was especially evident in the Ephemeroptera, all three orders exhibited this pattern. In contrast, our estimates of diel behavior, length of emergence period, and adult longevity varied considerably among closely related species. Because similar species shared similar return proportions but had different strategies for coping in the terrestrial system, success in the adult stage may be more complex than previously thought.

### Influence of diel behavior on return proportion:

Based on the regression analysis for adult EPT families and species in our system, a strategy of daytime emergence and return appears to be associated with returning to the stream safely. Conversely, nocturnal activity corresponds with lower proportions of adults returning to the stream. This is surprising for two reasons: One, previous research pertaining to predation of adult aquatic insects emphasized daytime visual insectivores such as birds (Nakano and Murakami 2001; Gray 1993), or other vertebrates (Sabo and Power 2002). Daytime predator-prey interactions are perhaps

more observable and thus more frequently remarked upon. And two, if low light conditions are more hazardous for aquatic insects, then through selection pressure we would expect to see more activity during the morning and afternoon hours. Yet, the consensus is that most mayflies (Edmunds and Edmunds, 1980; Friesen, et al. 1980), stoneflies (Hynes 1976), and caddisflies (Jackson and Resh 1991, Jackson 1988) are emerging and actively flying in search of mates at or just before dusk and continuing through the night. We observed a similar pattern in our system. In our diel samples, 64% of all insects caught were from traps set between 1700 to 0500. Other factors, such as cooler air temperature may be the reason for the greater numbers of adult aquatic insects after 1700 hours (Edmunds and Edmunds 1980, Jackson 1988). Jackson (1988) theorized that along Sycamore Creek in Arizona extreme high temperatures during the day might explain the high level of aquatic insect activity after dusk. He reported strong negative correlation between daily maximum temperature and daytime insect abundances. Temperature conditions were much less extreme in our temperate system.

While we saw a statistically significant correlation between return proportion and diel activity, a closer look at the patterns of both measurements at different taxonomic levels reveals a less conclusive relationship. We started with the assumption that the timing of such activities as emergence and oviposition flights are adaptations in response to local riparian conditions, such as high predation rates or non-optimal thermal conditions. If diel activity were an important determinant in surviving to oviposition, we would expect to see consistent patterns in  $P\{\text{night}\}$  and

P{return} among closely related species. Yet, species within the same family or genus were generally highly variable in their diel activity, but were remarkably similar in the proportion that returned to the stream (Table 5).

Differences within and between genera suggests that the timing of certain activities within a 24-hour period does not greatly influence the number of individuals of an adult population surviving until the time of oviposition. These diel preferences are most likely not controlled by local riparian conditions. Clearly, other factor(s) is/are exerting influence on adult EPT insects because P{return} estimates within each order vary greatly, yet the range narrows with each higher level of taxonomic resolution. Possible species specific factors might be morphological (e.g. size, coloration, the ability to feed), physiological-environmental (e.g. temperature tolerances), or behavioral (e.g. mating behavior, microhabitat selection). Future investigation in this area of aquatic insect behavior will require taxonomic resolution at least to the genus level. Our ability to predict survivorship and diel preference in the adult stage is severely limited given the wide range of values exhibited at family and order taxonomic levels.

Table 5: Variability of return proportion and diel activity by taxonomic level

<b>Taxonomic resolution</b>	<b>P{return}</b>	<b>P{night}</b>
Trichoptera (order)	high variability	high variability
within family	low	high
within genus	low	low
Plecoptera (order)	high	moderate
within family	moderate	moderate
within genus	low	moderate
Ephemeroptera (order)	high	moderate
within family	low	high
within genus	low	high

Emergence period and adult longevity:

Shorter emergence periods (Fig. 8) and shorter adult life stages (Fig. 9) were significantly correlated with P{return} for EPT species during the summer; however these results do not imply causality. Con-generic and con-familiar species exhibited

very similar  $P\{\text{return}\}$  but length of emergence period and adult stage varied. As with diel activity, links between length of the adult stage and emergence period on the one hand, and return proportion on the other, are not strong. Emergence period length and adult longevity are characteristics that can differ from species to species within a genus and perhaps from location to location within a species. The factor(s) affecting how many adults return to the stream, however, may be associated with genera, since species within a family have similar return proportions.

The 22 EPT species overlapped considerably in estimated length of emergence period, unlike our estimates of adult longevity where the species tended to segregate by order. Our initial hypothesis - that species with longer emergence periods would exhibit lower return proportion - appears to be confirmed (Fig.8). All species with emergence periods of at least 8 weeks had a  $P\{\text{return}\}$  of 0.31 or less, while seven out of the ten taxa with short (6.5 weeks or less) emergence periods had a  $P\{\text{return}\} > 0.36$ .

*Glossosoma penitum* had the longest emergence period of any species we investigated and far exceeded the duration of our sampling. Anderson and Bourne (1974) showed that the continuous emergence of *G. penitum* from March to November in Oak Creek in the Oregon Coast Range was actually two overlapping generations. Because they were the most abundant EPT species in our stream reach and returned in very low numbers ( $P\{\text{return}\} = 0.07$ ), they likely contributed the most, at least numerically, to riparian food webs during the summer. Similarly extended emergence

and return curves were observed for *Baetis spp.* (Appendix, Fig. 1), although we suspect this taxon to be at least three separate species.

The negative relationship between adult longevity and return proportion (Fig. 9) was driven by five caddisfly species combining long adult stages with low return proportions, and the three *Paraleptophlebia* mayfly species, all very short-lived in the adult stage and  $P\{\text{return}\}$  estimates exceeding 0.75. However, the relationship may be different when viewed strictly within an order. Among the six Trichoptera species longer adult stages are associated with slightly higher return proportions rather than lower (Fig. 9).

A cause of uncertainty in our data is associated with some estimates of adult longevity, especially with stoneflies. We could never be sure the first appearance of a given taxon in our pan traps was indeed the onset of return or simply a freshly emerged insect that had blundered into the wrong trap. With the overall low numbers of stoneflies caught we based some of our estimates on just a few individuals from our pan traps (Fig. 7). Plecoptera adult longevity is a function of whether they feed as adults for development of the eggs (Zwick 1990, Collier and Smith 2000). Adult feeding appears to be a species-specific characteristic (Hynes 1976), and there is very little existing data on North American stonefly species. For example, many European species in the family Nemouridae have adult stages lasting 3-8 weeks, with females sustaining themselves on nectar and fungi (Zwick 1990). Yet the nemourid stonefly we collected, *Zapada frigida*, appears to return in less than one week, an indication

that it probably does not feed. Greater precision in these estimates may require the rearing of individuals to the adult stage.

Relatively good published information exists on the length of the adult stage for North American mayflies. Because the temporal scale of our sampling schedule was not conducive to establishing our own estimates of longevity, we relied heavily on the work of those who have reared or made detailed observations (Lehmkuhl and Anderson 1970, 1971, Edmunds and Allen 1964, Jackson 1988). The mayfly's inability to feed as an adult limits this life stage (Williams and Feltmate (1992). Longevity across all mayfly species seem to range from less than one day, such as for some *Baetis* spp. (Jackson 1988, Wallace and Anderson 1996) to three days for *Epeorus (Iron) longimanus* (Edmunds and Allen 1964, Lehmkuhl 1968). For some species, e.g. *Epeorus (Iron) albertae* and *Dipheter hageni*, our estimates of adult longevity were based on published accounts of closely related species.

We had hoped, prior to analyzing our samples, that the curves generated would be relatively bell-shaped, of the same length, but different in their start date and magnitude (Harper et al. 1995). In most cases, however, the abundance data did not conform to this model, so we examined other characteristics to derive our own estimates. In theory, estimating longevity by the lag in time between the curves using either the start dates, the end dates, or the peaks does not pose any problems. When possible, we used all three to verify and substantiate our estimates. For example, the Trichoptera species *A. occidentis* (Fig. 5-G) had similar lag times between their emergence and return curves in their start dates and peaks, while *L. unicolor* (Fig. 5-

D) exhibited roughly the same longevity estimates with the time distance in start and end dates. Likewise, we have greater confidence in our longevity estimates for the Plecoptera species *Zapada frigida* (Fig. 7-A), *Chernokrilus misnomus* (Fig. 7-B), and *Sweltsa fraterna* (Fig. 7-C) than in other Plecoptera because lag times between start and end dates are similar. To our knowledge, no published accounts of adult longevity exist for the Trichoptera and Plecoptera species we examined, so no independent corroboration was possible.

Several species continued to emerge past the latest date for return (for example Fig 1-A, B), or, as was the case for *Suwallia* spp and *Epeorus (Iron) albertae* where return preceded emergence at our study site. A possible explanation for these phenomena is that these insects are flying upstream to oviposit to compensate for downstream drift during their larval stages. Species emergence cycles generally are temperature dependent – they start at lower elevation and proceed upstream (Williams and Feltmate 1992). Early returning flights could represent individuals from downstream that flew into our study reach before the local population was ready to emerge. Similarly, late developing local individuals could still be emerging after all oviposition flights into the area from downstream individuals had ceased.

#### Riparian predators:

Due to low abundance of insectivorous birds adjacent to our study site during the summer months we believe aquatic insect losses from bird predation were minimal. Other riparian bird surveys (Johnson and Haight 1985, Stahlecker et al.

1989) from drier ecosystems showed higher densities than our observations. A possible interpretation of our low numbers is that our field season may have started after most riparian birds had fledged their young and dispersed. Spiders, however, were numerous and appeared to be responding to the influx of prey from the aquatic system. We found many that had crawled up into the netting of our emergence traps and had fed upon aquatic insects that had not yet fallen into the tray. Since many web-spinning spiders operate on a 24-hour schedule (Gertsch 1949), their presence would not be a selective force for any particular diel patterns of emergence, swarming or oviposition behavior. Ambush spiders of the family Lycosidae (wolf spiders), which were frequently spotted scrambling over rocks along the bank, can likewise be active hunters during the day or at night, depending on species (Gertsch 1949). Most often we encountered ground spiders in the early morning and late afternoon when air temperatures were reduced.

The low P{return} of night-active aquatic insects might be related to bats foraging over water at dusk and at night. Their feeding was observed on several occasions, usually starting within a half-hour after sunset, but unfortunately, no formal data was collected. According to a study of bat foraging activity in two riparian areas in the Coast Range of Oregon, bats are most active just after sunset with a smaller peak just before sunrise (Hayes 1997), and foraging is positively correlated with minimum nightly temperature and insect biomass. Assuming a similar foraging pattern in our system the greater activity peak at sunset would have occurred during our 12-hour nocturnal sampling. In another study on bat and nighthawk prey

selectivity large (>5mm) caddisflies were the most preferred prey items (Brigham 1990). Insects smaller than 5 mm were under-represented in bat and nighthawk diets, and Brigham hypothesized that these insects were below the minimum threshold size required for efficient echolocation. Though exact measurements were not made, most of the caddisflies in our study were > 5 mm, with the exception of *Agapetus occidentis* and members of the Hydroptilidae. Because *A. occidentis* were day-active, it was less available as prey for bats. The minute caddisflies in the family Hydroptilidae exhibited the highest return proportion of any taxa in our study ( $P_{\text{return}} > 1.0$ ). Not all large taxa had low return proportions. Most of the individuals in the families Rhyacophilidae ( $P_{\text{return}} = 0.41$ ) and Hydropsychidae ( $P_{\text{return}} = 0.30$ ) exceeded 10 mm in length, and the large perlodid stonefly *Chernokrilus misnomus* had the highest  $P_{\text{return}}$  among stoneflies (0.99).

Given high abundance and low  $P_{\text{return}}$ , caddisflies contribute the most to net export to the adjacent riparian system during the summer, mayflies contribute less and stoneflies very little. The most abundant caddisfly species, *Glossosoma penitum*, exhibited one of the lowest proportion of returning adults. There are several possible explanations that may singly, or in combination, explain why caddisflies are more vulnerable in the Lookout Creek basin. For one, the overall duration of the adult stage is generally longer for caddisflies than for stoneflies and certainly for mayflies, increasing their overall vulnerability to predation. Though caddisflies are not synchronous at emergence, their higher densities may also allow predators, such as bats, to key into emergence events when concentrations are highest.

Environmental factors:

In a desert stream system (Sycamore Creek, Arizona), overall aquatic insect  $P_{\text{return}}$  was 0.03 - much lower than what we observed (Jackson and Fisher 1986). They also reported a  $P_{\text{return}}$  of 0.01 for two different *Baetis* species, again much lower than our estimate for *Baetis* (0.07). The larger traps used in their study, 1.0 m<sup>2</sup> catch nets placed in the water to collect returning insects, may or may not have been as efficient as our pan traps, but we do not believe this accounts for the great difference in measured return proportion between the two studies. We suggest that the differences in estimates can be attributed to the larger productivity gradient from stream bank to upslope areas in their xeric riparian systems, where prey and insectivores such as birds are much more concentrated along watercourses.

On large rivers in Eastern Oregon, where dry conditions and land use practices preclude the development of a wide riparian forest buffer, it is common to observe hundreds of swallows and other birds simultaneously foraging on clouds of aquatic insects during their emergence events. Such phenomena are rarely witnessed on rivers of similar size in the much wetter western portion of the state. Riparian and upland forest structure in intact old-growth Douglas-fir forests are both complex, but in habitat quality for birds they are perhaps equally good. Comparing upslope and riparian areas in Western Oregon, McGarigal and McComb (1993) found greater avian diversity in forested upslope habitat than along forested sections of streams. Likewise,

flying insect density gradients perpendicularly away from Lookout Creek are probably much less pronounced than along desert streams, although to our knowledge this has never been investigated. We speculate that greater interaction strengths exist in desert riparian systems where insectivores are more dependent on aquatically derived prey than in our mesic, temperate system.

There is strong evidence that echo-locating bats in the Pacific Northwest use riparian corridors in forested, montane areas more than interior forest habitats as foraging sites, because clutter from trees and other vegetation is reduced, which might otherwise interfere with prey detection and capture (Grindal 1998). Increased use of riparian areas in foraging and a diet preference for large caddisflies may explain the low return proportion of night-active caddisfly species. We regret not monitoring bat activity at our study site, but encourage others to investigate and quantify the flux of energy from water to land through bats.

#### Adult insect behavior:

Hynes (1976), in his synthesis on the biology of stoneflies, discusses the preponderance of stonefly species that emerge and mate in low light conditions. A majority of the stonefly species we investigated, however, showed the opposite behavior. This apparent contradiction can be partially explained by our sampling methodology. Our emergence traps were designed to capture flying insects lifting up out of the surface film of the stream. Many stoneflies emerge out of the water not from the water surface in mid-stream as mayflies and caddisflies, but by crawling up

rocks protruding from the water surface or out along the banks (Hynes 1976). Hence, they are most likely underrepresented in our samples. Some of our specimens undoubtedly managed to climb up into the emergence traps from the support frame. In some cases we deliberately placed some exposed rocks under our emergence traps to insure the capture of those species that require a dry surface platform for lifting into the air. Likewise, oviposition behavior may have made some adults less vulnerable to pan traps, which are designed to capture insects falling in or dimpling their abdomens to extrude eggs directly into the water. For example, we caught several large perlid stoneflies (primarily *Doroneuria baumanni* and *Calineuria sp.*) in our emergence traps, but none in our pan traps. Either this family of stoneflies is extremely vulnerable in the adult stage or their return behavior avoided capture in the pan traps. Among Trichoptera, some limnephilids lay their eggs in moist soil above the water line during summer low flows (Wallace and Anderson 1996). Eggs then hatch when fall rains raise water levels. Pan traps would not capture adults employing this kind of oviposition behavior. The specific oviposition behavior of the perlid species in our study area is not known.

Discrepancies between estimates of mayfly P<sub>night</sub> from emergence and pan traps (0.62) and from hanging sticky traps (0.35) can be explained by typical mayfly behavior. Individuals emerging around dusk (after 1700) are likely molting into imagoes during the night. Mating swarms would typically take place during midday or afternoon (Needham et al. 1935, Brittain 1982), when they might blunder into our hanging sticky traps, and are ready to oviposit soon after. As they dimple their

abdomen to release eggs into the water the females again become vulnerable to in-stream traps, in this case our pan traps, and this activity might extend again into the evening hours. There was not much information in the scientific literature as to the fate of males after mating, but it can be assumed that many expire over water, with some falling into our pan traps. We believe the sex ratio in our traps approximately 55-60% were females, was not significantly sex biased.

Several limitations of this study became apparent as the data was analyzed. For example, a more comprehensive protocol for sampling other riparian insectivores such as bats, may have yielded a better understanding of whether predation pressure plays a role in the timing of key events in the adult stage of aquatic insects. Also, our intensive sampling was limited to a short section of a stream and for a relatively short duration. Future sampling should include spring emergence events and several well-spaced sections of stream to observe how longitudinal gradients with more heterogeneous terrestrial and aquatic habitats may influence return proportions.

## Conclusion

In summary, the similarity of our estimates of return proportion in closely related species suggests that the factor(s) influencing how many individuals survive long enough to mate and return to the stream to oviposit are shared at the genus level. Preferences in the diel timing of emergence and return do not seem to be shared behavioral traits among taxa within family or even genus, and therefore likely do not greatly influence return proportion.

The return proportions we calculated at the order, family, genus and species levels are entirely new information for these taxa, which can be used as benchmarks for other studies investigating the aquatic contribution to riparian food webs.

Research on the natural history of aquatic insects has not been in vogue for aquatic ecologists for many years, as evidenced by the paucity of published articles on the topic over the last few decades. The existing gaps of such basic information as adult longevity, diel periodicity, and mating and oviposition behavior for many species of aquatic insects prevent us from interpreting our data with certainty. Several life history strategies of the EPT taxa examined in our study represent in most cases information that has not been previously available.

By tying together our return proportion results with specific life history traits we tried to discern if, and to what degree, return success is dependent on these traits. Our study begins to address speculations that nocturnal timing of emergence and return, shorter adult stages, and short, synchronized emergence periods are adaptations

to avoid predators (Edmunds and Edmunds 1980). While the data did not provide any conclusive evidence, some of the results were surprising. Contrary to what we expected, daytime insects fared somewhat better than those inclined toward activity at night, and most of the stoneflies in our study reach were active during the day.

Our data also show interesting taxonomic patterns between the life history parameters of return proportion, emergence period length, and adult longevity. Emergence period length and adult longevity appear not to be shared traits among congenics, but they may be contributing factors in determining a species' return proportion. None of the major points made in this study would have become apparent to us had we not made the effort in identifying our EPT to species when we could. We therefore recommend that any future studies of this nature provide taxonomic information at least to the genus level.

The diversity of strategies employed by EPT adults at our study site appears to be much greater than for species at lower and higher latitudes where harsher climates exist. In hotter, drier climates almost all aquatic insects exhibit nocturnal behavior and highly synchronized, short adult life spans to minimize exposure (Jackson 1988). The opposite occurs in the far north where cold night-time temperatures cause the majority of insects to be most active during the daytime (Edmunds and Edmunds 1980). The relatively mild climatic conditions of western Oregon may not be controlling these life history parameters to the same extent, allowing for different and less rigid behaviors among even closely related species.

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## **APPENDIX**

Table 1. List of birds from 50m x 50m point counts, with total number of individuals and number of times observed, 6-21-01 to 9-11-01.

<u>Common Name</u>	<u>Species Name</u>	<u># of birds</u>	<u># of times birds seen</u>
Chestnut-backed chickadee	<i>Peocile rufescens</i>	24	11
Winter wren	Troglodytes troglodytes	11	8
Hammond's flycatcher	Empidonax hammondii	6	5
Swainson's thrush	Catharus ustulatus	4	3
Yellow-rumped warbler	Dendroica coronata	4	2
Hermit warbler	Dendroica occidentalis	3	3
Steller's jay	Cyanocitta stelleri	3	3
Western tanager	Piranga ludoviciana	3	2
Pine siskin	Carduelis pinus	2	1
Brown creeper	Certhia americana	2	1
House wren	Troglodytes aedon	1	1
Golden-crowned kinglet	Regulus satrapa	1	1
Song sparrow	Melospiza melodia	1	1
Willow flycatcher	Empidonax traillii	1	1
Red-breasted nuthatch	Sitta canadensis	1	1
	<b>Total</b>	<b>67</b>	

Fig. 1 Emergence and return curves for *Baetis spp.* (Baetidae: Ephemeroptera) from 6-25-01 to 9-20-01.

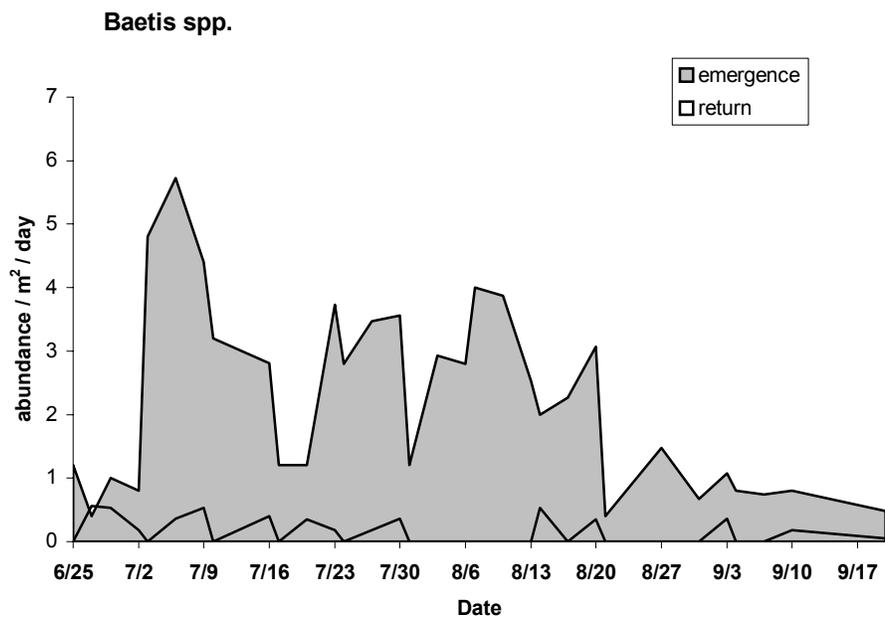


Fig. 2 Emergence and return curves for *Dipheter hageni* (Baetidae: Ephemeroptera) from 6-25-01 to 9-20-01.

### Dipheter hageni

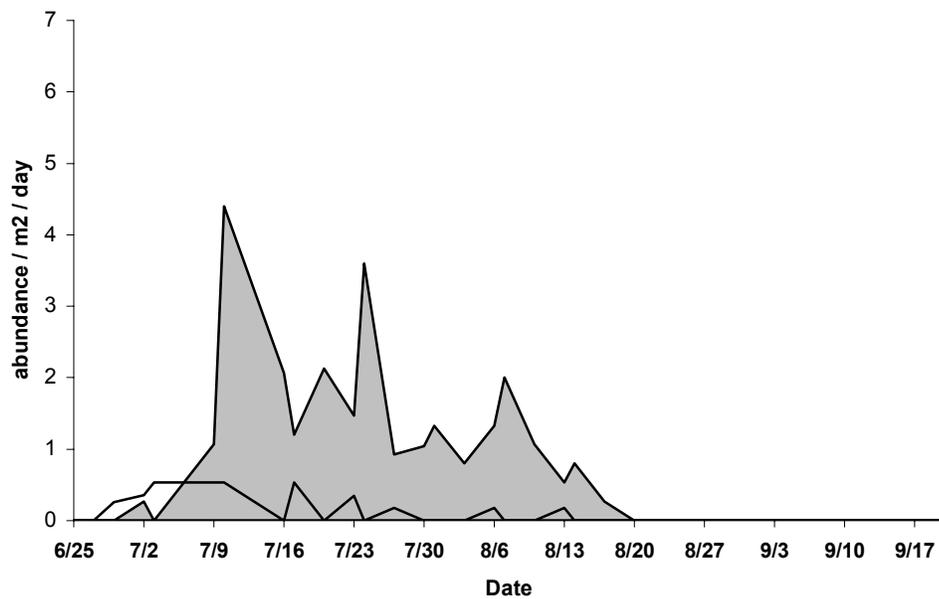


Fig. 3 Emergence and return curves for *Epeorus (Iron) longimanus* (Heptageniidae: Ephemeroptera) from 6-25-01 to 9-20-01

**Epeorus (Iron) longimanus**

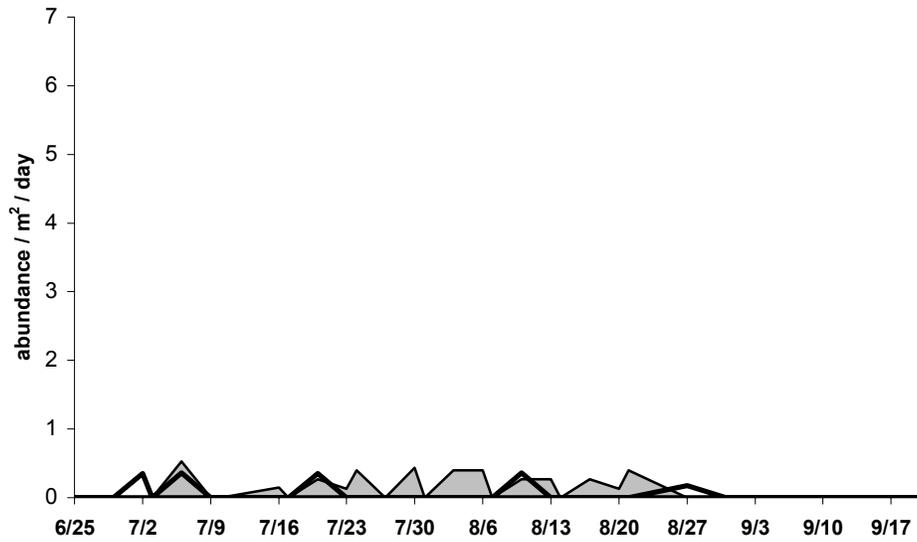


Fig. 4 Emergence and return curves for *Epeorus (Iron) albertae* (Heptageniidae: Ephemeroptera) from 6-25-01 to 9-20-01.

**Epeorus (Iron) albertae**

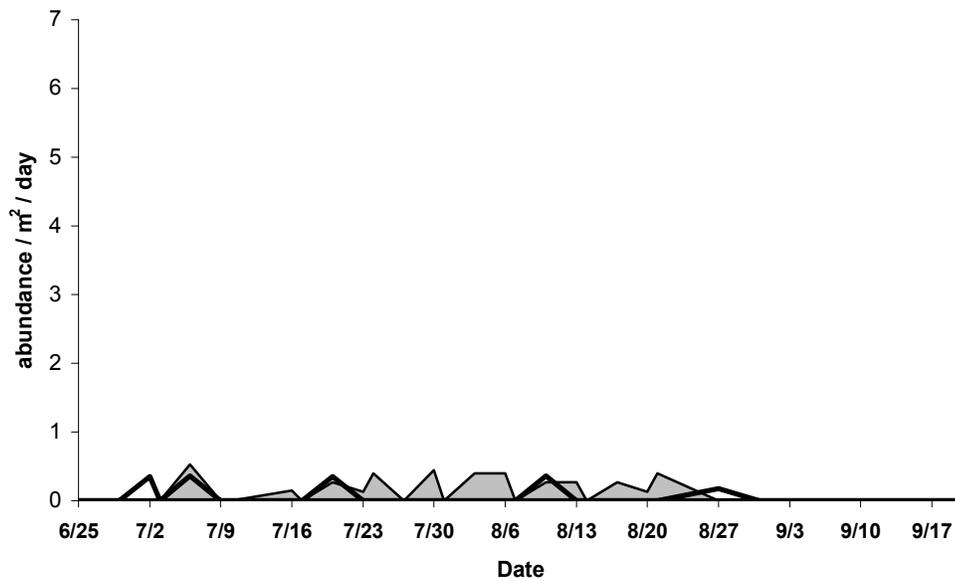


Fig. 5 Emergence and return curves for *Cinygmula reticulata* (Heptageniidae: Ephemeroptera) from 6-25-01 to 9-20-01.

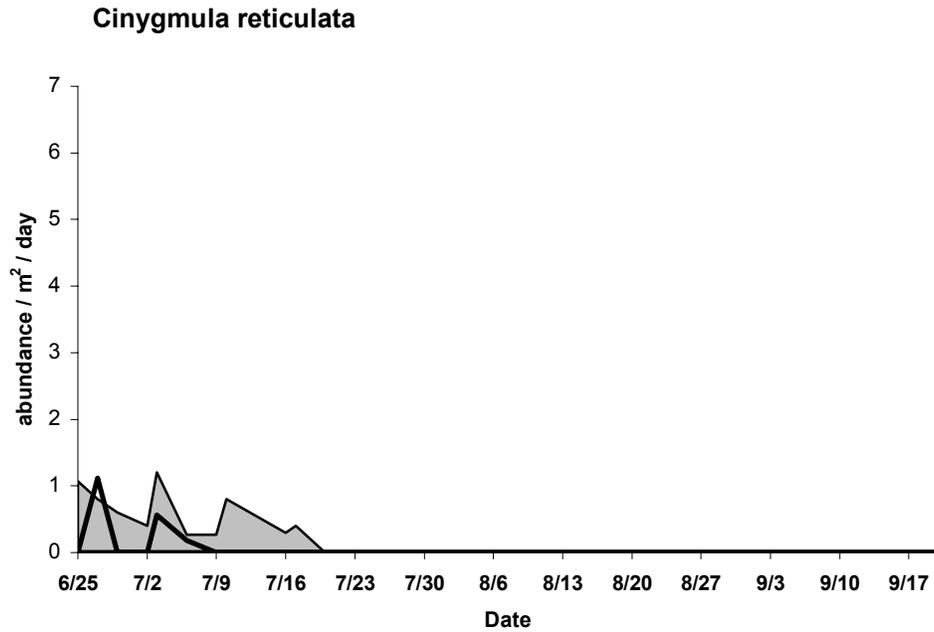
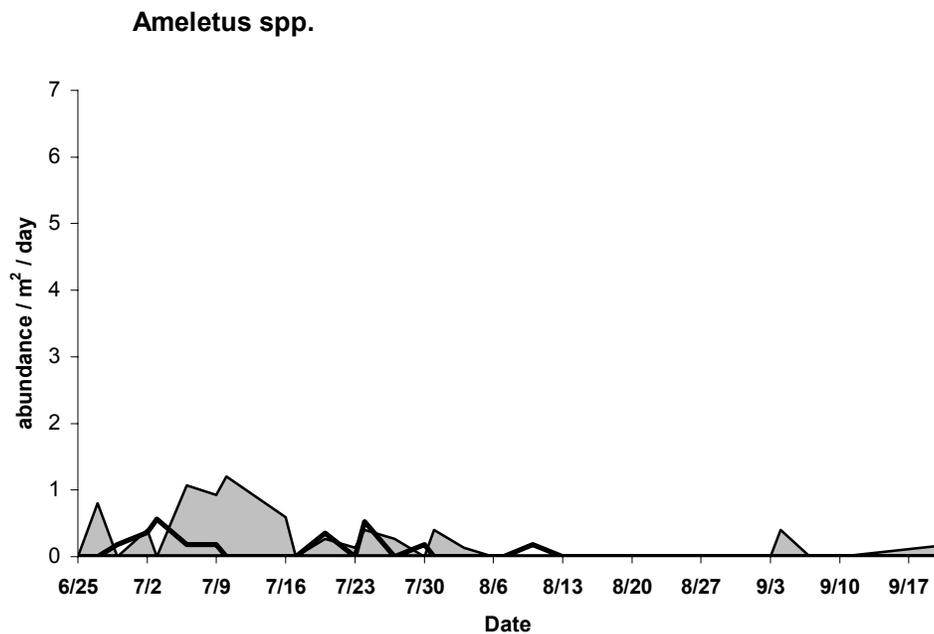


Fig. 6 Emergence and return curves for *Ameletus spp.* (Ameletidae: Ephemeroptera) from 6-25-01 to 9-20-01.



Note: Complete emergence and return trap data can be reviewed and downloaded at the following URL:

[www.fsl.orst.edu/lter](http://www.fsl.orst.edu/lter)