

Variations in the trophic ecology and densities of *Ascapthus truei* in two
streams with different timber management histories

by

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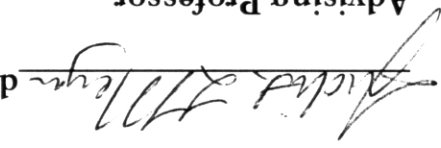
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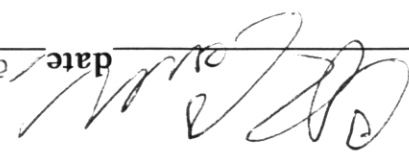
Variations in the trophic ecology and densities of *Ascarphus truei* in two streams with different timber management histories

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Abstract

I examined the feeding ecology of tailed frogs (*Ascaphus truei*) and identified ways in which the populations and food resources of this riparian and old-growth associate varied between two streams with different timber management histories. Data were collected during July and August 1998 from two third order streams in the Willamette National Forest in western Oregon. Mack Creek drains a pristine watershed in the H.J. Andrews Experimental Forest; Pasture Creek is west of the Sisters Wilderness Area, and the sampled reach is 3 km downstream from several small clear-cuts. Both sites historically supported *Ascaphus truei*. Feeding ecology was investigated by gut flushing and examining the gut contents of 45 frogs from Mack Creek. Population and range data for individual tailed frogs were derived from mark-recapture studies on Mack and Pasture creeks. Tailed frog populations were larger in Mack Creek than in Pasture Creek with 39 ± 2 and 13 ± 1 individuals respectively within comparable 50 m stream reaches. Individuals ranged over very short reaches and exhibited high site fidelity in both streams. Average ranges were 4.0 ± 0.9 m of stream in Mack Creek and 2.5 ± 1.5 m in Pasture Creek. In-stream food sources accounted for 37% of the mass of gut contents, whereas spiders and terrestrial insects accounted for 20% and 34% respectively. Dependence on the stream for food and apparent philopatry suggest that *Ascaphus* is vulnerable to natural and anthropogenic disturbances. Moreover, the lower epilithic biomass, algal biomass, and aquatic invertebrate biomass in Pasture Creek suggests effects on *Ascaphus* food resources resulting from the clear-cut. The higher water temperature and increased sedimentation in Pasture Creek may also have affected the tailed frog population. Differences in water chemistry between watersheds was probably not a cause of the observed disparity in tailed frog populations between Mack and Pasture creeks, but differences in temperature, sedimentation, and aquatic food resources could be responsible.

INTRODUCTION

Understanding the spatial and temporal effects of timber management on riparian associated species is a research priority in the Pacific Northwest (Cissel et al. 1998, Smith et al. 1997). Issues such as the impact of timber removal on stream-dwelling amphibian populations in the Cascades Range of the Pacific Northwest are not well understood, and knowledge of species-habitat interactions in general is lacking (Smith et al. 1997). Many sensitive species of amphibians such as the tailed frog (*Ascaphus truei*) and the Olympic salamander (*Rhyacotriton olympicus*) are riparian and old-growth associates (Gomez and Anthony 1996, Welsh 1990). Consequently, understanding the effect of timber management on these animals and their habitats is essential to their preservation. Conservation of biodiversity is a stated priority of land managers in the Pacific Northwest (Smith, et al., 1997), and to be successful, it is necessary to understand the nature of the dependence of these animals on mature forest environments (Smith et al. 1997). An awareness of the factors that limit these animals to old-growth and riparian habitats will enable implementation of improved management practices.

Analyses of the autecology and ecological associations of amphibians (Smith et al. 1997) that clarify species-habitat interactions in riparian zones (Cissel et al. 1998) are of interest because amphibian biomass exceeds avian and small mammal biomass in some systems (Burton and Likens 1975). In Oregon, the Pacific giant salamander (*Dicamptodon tenebrosus*) accounted for 79% of total biomass in one stream (Murphy and Hall 1981), and *Ascaphus* may achieve densities as high as 4.5/m² (Bury 1988) or 70 individuals per 60 m (Metter 1964). Thus, these animals may comprise an important energy pathway (Corn and Bury 1989, Bury 1988). However, the low-order, high-gradient, mostly non-fish-bearing streams that *Ascaphus* prefers (Bury 1968) have received only limited scientific attention. The current knowledge of *Ascaphus* and other riparian amphibian species is inadequate (Smith et al. 1997) because much of the research done in stream ecosystems of the

Pacific Northwest has historically dealt with commercially important salmonid fishes (Smith et al. 1997). There are few data available on the effects of timber removal on other riparian-associated or obligate species. Thus, special attention to amphibians is warranted.

This study investigated the autecology of tailed frogs (*Ascaphus truei*) and the effects of clear-cutting on downstream populations of *Ascaphus* and its food resources in the Cascades Range in western Oregon during July and August 1998. The autecological observations focused on the tailed frog's feeding ecology, movement, and densities. I also compared abiotic and biotic habitat characteristics such as stream temperature and standing stock of algal biomass between two streams, Mack and Pasture creeks. Mack Creek was the reference stream, representative of undisturbed old-growth forests within the McKenzie River drainage. Pasture Creek's watershed was recently clear-cut approximately 3 km upstream from my sampling reach.

Trophic Ecology of *Ascaphus truei*

One objective of this study was to gain a better understanding of the feeding habits of *Ascaphus truei*, particularly the extent to which *Ascaphus truei* populations depend on terrestrial versus aquatic food resources. Several investigators (e.g., Metter 1964) have reported that *Ascaphus* utilizes a variety of food types from both aquatic (in-stream) and terrestrial habitats. However, the precise nature of this dual dependence is not known because early data sets report abundances of prey items rather than prey biomass. Since both resources are impacted by timber harvest, an investigation of the feeding ecology of *Ascaphus* should yield valuable insights into the possible effects of various timber management regimes on this species.

Intersite Comparison

The second objective was to analyze potential effects of timber management in the headwaters of a stream on the abundance and food resources of downstream *Ascapbus* populations. Mack Creek, an old-growth watershed in the H.J. Andrews Experimental Forest, provided a reference for comparison with Pasture Creek, which had a portion of its headwaters clear-cut in 1992. The lowest patch of clear-cut forest was approximately 3 km upstream from the study site. Each watershed historically supported populations of *Ascapbus* although casual observations suggested a decline in the abundance of *Ascapbus* in Pasture Creek after 1992 (Joseph Beatty, Dept of Zoology, Oregon State University, pers. comm.). I hypothesized that declining food availability combined with the adverse effects of increased temperature and sedimentation could be responsible for the decline (Brown and Krygier 1970).

Deforestation changes more than the structure of a stream's riparian zone. In-stream and terrestrial habitats receive more sunlight and experience higher temperatures, increased sediment loads, and altered hydrology (Corn and Bury 1989, Brown and Krygier 1970). Stream chemistry also changes; for example, nitrate (NO_3) concentrations increase (e.g., Likens et al. 1970). These effects are local consequences of timber removal that can be transmitted downstream. For example, water temperatures may drop by as much as 7°C within 122 m of the point where a stream re-enters a forested environment from a clear-cut tract of land (Brown and Krygier 1970). Long-term effects of logging included a reduction of coarse woody debris (CWD) inputs to a stream and reduced primary productivity because of decreased insolation once the dense early successional canopy begins to grow (e.g., Hawkins et al. 1992, Bury and Corn 1988). CWD and autochthonous food resources are important for the invertebrates, which are the prey of tailed frogs. The indirect effects of increased nitrate concentration, increased sedimentation, reduction of allochthonous inputs, and reduced primary productivity in streams are more likely to cause changes in downstream amphibian

populations than water temperature or insolation. Thus, this study examined the temperature, water

chemistry, and biomass of each trophic level in Mack and Pasture creeks. Differences were

attributed to result from the clear-cut in the headwaters of Pasture Creek.

These investigations of tailed frog feeding ecology and the comparison of Mack and Pasture creeks complement each other. Gut analyses reveal the degree to which tailed frogs rely on aquatic versus terrestrial sources of production, and the mark-recapture analyses provide information on densities and site fidelity. Each of these attributes influences the species' vulnerability to disturbance. Linking these components helped identify promising areas for further investigation.

Natural history of *Ascaphus truei*

The tailed frog was first described by Leonhard Stejneger in 1899 (*Ascaphus truei* Stejneger) (Noble and Putnam 1931). It is the only extant species in its taxonomic family Ascaphidae, and it is closely related to the Leiopelmatidae of New Zealand (Pough et al. 1998, Zug 1993). Both families are sometimes lumped into one and are considered relictnal sister taxa of all other extant frogs. Blaustein et al. (1995) referred to the tailed frog as the "most primitive of all living frogs".

Ascaphus is endemic to the Pacific Northwest where isolated populations and philopatry make it susceptible to local extinction (Bury 1988a,b, Bury 1968). The geographic range of *Ascaphus truei* includes montane portions of northern California, Oregon, Washington, Idaho, Montana, and British Columbia (Nussbaum 1983). Within these areas, it may be found at elevations ranging from sea level to 2000 m (Blaustein et al. 1995) in cold high-gradient streams, but it is not found in the drier desert regions in the rain shadow of the Cascades (Nussbaum 1983).

Populations of tailed frogs are isolated and disjunct (Nussbaum 1983) because of stenotypic habitat tolerances (e.g., Claussen 1973a,b) and extreme philopatry (Daugherty and Sheldon 1982). Movement is influenced by climatic conditions (Metter 1964), and most dispersal occurs during cool

wet weather rather than during dry warm weather (Daugherty and Sheldon 1982). Metter (1964) reported finding *Ascapbus truei* under large rocks in streams during the winter months, and Daugherty and Sheldon (1982) reported that the species is restricted to streams during dry summer months. During periods when conditions are conducive to movement, *Ascapbus truei* remains philopatric and as much as 71% of a population may remain in the same 20 m stream reach during successive years (Daugherty and Sheldon 1982). Tailed frogs have never been reported to range more than 137 m from a stream (Metter 1964). Consequently, populations are genetically isolated and disjunct (Welsh 1990), and recolonization of disturbed areas is usually slow (Blaustein et al. 1995, Daugherty and Sheldon 1982). The extreme philopatry (Daugherty and Sheldon 1982) has been connected to local declines in *Ascapbus* populations (Bury 1988).

Habitat selection by *Ascapbus* is also a result of its stenotypy (Claussen 1973a,b). Tailed frogs are the most cryophilic amphibian species in North America, requiring stream water temperatures below 16° C (Brown 1975, Claussen 1973a, Metter 1964). In laboratory experiments, *Ascapbus truei* tadpoles are more tolerant of warm water temperatures than adults (Claussen 1973a). However, in nature the tadpoles are most often found in stream reaches cooler than 10° C for first year tadpoles and between 10° and 22° C for second year tadpoles (Brown 1975, Vlaming and Bury 1970). The tailed frog also loses water faster than any other North American frog (Claussen 1973b). Thus, *Ascapbus truei* is most often found in undisturbed streams in old-growth and mature forests (Gomez and Anthony 1996) where stream temperatures are cool and riparian microclimates are humid. Cold humid environments are necessary for survival at all stages of the tailed frog's life history (Claussen 1973a,b, Metter 1964), and the species may be adversely affected by timber removal (Bury 1988) which may cause habitats to become drier and warmer (Brown and Krygier 1970). However, *Ascapbus truei* is occasionally found in young stands or in streams traversing clear-cuts (Anthony and Gomez 1996, Corn and Bury 1989, Bury 1968).

The reproductive cycle and life history of the tailed frog are specially adapted for lotic environments (Pough et al. 1998, Zug 1993). The method of mate selection is unknown because the frogs do not possess vocal chords or tympana (Pough et al. 1998, Zug 1993). Nevertheless, tailed frogs mate in the water where fertilization of the female's eggs takes place internally following mating sessions that may last as long as 30 hours (Metter 1964). During this period of inguinal amplexus, the male grapples the female into a position that allows him to insert his intermittent organ ("tail") into her cloaca. This behavior is most commonly observed during the early summer (Noble and Putnam 1931). Internal fertilization is believed to be a primitive trait of frogs (Blaustein et al. 1995) that has been retained in tailed frogs to facilitate copulation in an environment where swift currents might otherwise wash away sperm before fertilization can occur. The intermittent organ, which looks like a "tail" and gives the tailed frog its common name, is not a penis (Noble and Putnam 1931), but it is nevertheless only present on the male's body. Sperm from the male may be stored in the female's body for several months and the female lays her eggs under rocks in late July. Later in the summer, the slow-developing eggs hatch and fusiform tadpoles emerge. They are specially adapted to the stream environment; for example, they have an oral disk that allows them to attach to substrata in order to avoid being swept downstream by the current. The larval stage may last up to three years, but larvae in some populations in the Coast Range may metamorphose at the end of the second year (Noble and Putnam 1931).

The feeding ecology of *Ascaphus truei* is poorly documented in comparison to other traits. Tailed frogs are generalist predators that hunt at night, sometimes ranging several meters from the stream if the weather is cool and wet (Nussbaum et al. 1983). Several investigators have reported that *Ascaphus* utilizes a variety of food resources from both aquatic (in-stream) and terrestrial habitats, and it is generally accepted that *Ascaphus* "eats what is available" (Metter 1964). Thus, the diet may commonly include a variety of aquatic insect larvae, spiders, beetles, snails, and flies. There

is no documented evidence of a preference for a particular food type. Food is obtained by lunging toward prey that approaches too near, and this behavior is attributed to the primitive morphology of the tailed frog's tongue. The tongue of the tailed frog is attached at the rear of the mouth rather than the front as in most other frog species (Pough et al. 1998). Thus, the tailed frog can not catch airborne insects like some other anurans.

Tadpoles are herbivorous and scrape diatoms from submerged rock surfaces with specialized mouth parts (Blaustein et al. 1995). At times, they may be the dominant herbivore in some streams (Lamberti et al. 1992). Their mouth morphology allows them to emerge from the stream (Pough et al. 1998) to feed upon periphyton growing on rocks in the spray zone (Blaustein et al. 1995). Gut analyses revealed that the tadpoles' primary food source is diatoms, but high amounts of pollen and a few very small insects have also been found in tadpole guts (Metter 1964).

Tailed frogs are threatened by several predators. Reports attribute mortality to predation by garter snakes (*Thamnopsis elegans* and *T. sirtalis*), Pacific giant salamanders (*Dicamptodon tenebrosus*) (Bury 1988), foothill yellow-legged frogs (*Rana boylei*) (Bury 1968), and cut-throat trout (*Salmo clarki*). Although this list is probably incomplete, each of these known predators may consume either adult tailed frogs or tadpoles.

Natural and anthropogenic sources of disturbance may also cause mortality of tailed frogs and adversely affect their populations. The disappearance of tailed frogs from streams traversing clear-cut forests is well documented (e.g., Blaustein et al. 1995, Metter 1964). Corn and Bury (1989) have addressed broad temporal and spatial effects of timber removal on tailed frogs, and they found that sedimentation adversely affects tailed frog populations. Results from other studies support the findings of Bury and Corn and identified sedimentation of streams as an important factor affecting tailed frog populations (Welsh and Ollivier 1998).

Other consequences of disturbance have also been identified (e.g. Brown and Krygier 1970). *Asaphus truei* populations depend on terrestrial and aquatic food sources, so Bury and Corn (1988) hypothesized that timber removal might alter food availability and food quality for tailed frogs

because clear-cutting changes the structure of aquatic invertebrate communities in streams (Hawkins et al. 1982). These changes in the stream ecosystem may result from increases in stream water temperatures (Brown and Krygier 1970) and altered stream water chemistry (Likens et al. 1970). Elevated stream water temperatures are also thought to directly affect tailed frogs (Brown 1975) because the species is stenothermal (Clausen 1973a). Moreover, its philopatry may exacerbate the detrimental effects of habitat alteration by impeding recolonization of affected areas (Daugherty and Sheldon 1982)

METHODS

Site descriptions

Asaphus truei populations were studied in two streams: Mack Creek, in the H.J. Andrews Experimental Forest, Oregon, and Pasture Creek, a tributary of Horse Creek near Cougar Reservoir, Oregon. These two streams were chosen because each has been the focus of previous investigations of tailed frog populations and because their watersheds have similar physical attributes but different timber management histories.

At the landscape scale, Mack and Pasture creeks are comparable in terms of geography and geology. They are both located on the windward, southern portion of the Cascades Range within the Willamette National Forest in southwestern Oregon. Moreover, both study reaches are on north-facing slopes and the dominant vegetation and light regimes are similar and representative of the low order streams that occur throughout the Cascades Range. The bedrock is basalt, and the soils in both watersheds gave rise to old-growth stands dominated by Douglas-fir (*Pseudotsuga*

menziesii) mixed with western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). In areas with well-drained soils, the understory along each stream was composed of a mix of vine maple (*Acer circinnatum*), broadleaf maple (*A. macrophyllum*), huckleberry (*Vaccinium* spp.), Pacific rhododendron (*Rhododendron macrophyllum*), azaleas (*Rhododendron* spp.), and Oregon grape (*Berberis* spp.). However, areas characterized by moist soils were dominated by devil's club (*Oplopanax horridum*), salmon berry (*Rubus spectabilis*), and several unidentified ferns.

The study streams were also comparable at the reach scale. Mack Creek had a slightly higher discharge than Pasture Creek, but both streams were third order within the study reach and drained watersheds of similar area (Table 1). Discharge varied in both streams in response to evapo-

transpiration on a daily basis as well as a general lack of rain during the study period. Thus, flow declined between visits to the study areas. The channels were narrow with steep sides, and the riparian zones were likewise very narrow. The mature forest canopy over both streams was characteristically patchy, and light penetration to the streams varied spatially.

The primary difference between streams was in their history of timber management. Mack Creek drains a reference watershed that has never had timber removed. In 1992 the top of the Pasture Creek watershed was cut and reforested with Douglas fir seedlings. The cut areas consisted of several patches of unknown areas situated approximately 3 km upstream from the study area and 1 km below the watershed divide. Because tailed frogs prefer second and third order streams rather than the small, occasionally ephemeral, first order streams that flow through the clear-cut patches on this watershed, the study site was necessarily lower than the managed tracts of forest.

Ascaphus truei trophic ecology

The gut contents of frogs in Mack Creek were examined to determine the extent to which *Ascaphus* relies on various food sources. Frogs were collected from a reach immediately above the

mark-recapture study reach. Gut contents were obtained by flushing the guts of frogs with water until their contents had been regurgitated. Samples were transferred to scintillation vials and stored in 70% ethanol (Hawkins et al. 1982) prior to sorting and ashing. The gut contents from each frog were sorted into five categories: aquatic larvae, emerged aquatic adults, arachnids, other terrestrial organisms, and unknown. Some researchers have included the emerged aquatic adult insects with terrestrial food resources (Parker 1994), but the categories were left separate in this study because a major goal was determining the importance of aquatic production versus terrestrial production in meeting the energy requirements of *Asaphus trui*.

Intersite comparison

Abiotic factors: Discharge estimates were taken from the gauge on Mack Creek and were

provided by Patricia Zaradic for Pasture Creek (Patricia Zaradic, University of Pennsylvania, pers. comm.). Discharge was measured just before the first mark-recapture session on each stream, and hence the values recorded are maximum values because the stream flow in both Mack and Pasture creeks declined slowly during the summer. Water and air temperatures were recorded at the

beginning of sampling sessions.

Water samples were collected for chemical analyses from the thalweg at 60% depth and were filtered in the field using Whatman GF/F filters. Filtered samples were placed on ice and frozen until analyses could be completed using standard methods for analysis of ammonium (NH_4^+), nitrate (NO_3^-), and soluble reactive phosphorus (SRP). Mack Creek water chemistry was provided by the Lotic Intersite Nitrogen eXperiment (LINX) for the pre-release date in mid-July at 8 points along a 220 m reach immediately upstream from the study site (J. Tank, University of Illinois at Champagne-Urbana, pers. comm.). Two 1 liter water samples from the top and bottom of the study reach were

collected in early August for Pasture Creek, and two replicates from each location were analyzed on an Alpkem RFA-300 using standard methods.

Food resources: I measured the availability of food resources for *Asaphus truei* in Mack and

Pasture creeks by assessing standing stocks of epilithon, algae, and aquatic invertebrates. Epilithon and chlorophyll-a samples were collected by scraping the biofilm off a known area of submerged rock. One sample was taken for each of these compartments at 5 m intervals along the 50 m study reach (n=11 in each stream). Rocks were selected haphazardly and included all sizes (i.e. cobble, boulder, and bedrock). The scraped samples were stored in specimen cups for transport to the lab where they were filtered onto pre-ashed, pre-weighed Whatman GF/F glass fiber filters. Epilithon samples were dried and ashed immediately to obtain AFDM. Chlorophyll samples were frozen, shipped to the University of Georgia, and analyzed for chlorophyll-a using standard methods.

(Steinman and Lambert, 1996). Comparisons between streams were conducted using t-tests.

Aquatic invertebrate biomass was sampled using a Surber sampler (Hawkins et al. 1982).

Samples were taken from each stream at 5 m intervals (n=10 in each stream). The samples were placed in labeled ziplock bags, preserved with 70% ethanol in the laboratory, and picked for all

invertebrates. Invertebrates were ashed to obtain ash-free dry mass following the methods in Hauer and Lambert (1996). Statistical comparisons were performed using a t-test.

Demography: I determined the population size of *Asaphus truei* in Mack Creek by conducting

a census via a mark-recapture study in a 50 m reach of stream. I captured frogs by hand during two-hour timed collection periods beginning approximately an hour after sunset. Collection during

twilight hours was avoided in order to allow tailed frogs ample time to emerge from their day-time retreats. The timing clock was stopped while handling captured frogs; thus, the two hour timed

collection often spanned 2.5 to 3 hrs of real time. The animals did not seem affected by my lights and were easily captured by gently scooping them off their perches by hand. For each capture, I

recorded the transect (meter mark), habitat, sex, snout-vent length (SVL) and mass of the specimen, marked them with individual toe-clips, and released the frogs where they were captured. New

captures were marked throughout the study. Sampling took place over a period of 23 days on Mack Creek (23 July – 15 August) and 27 days on Pasture Creek (22 July – 17 August) with 3 to 4 days between sampling sessions. This schedule allowed for eight sessions on Pasture Creek and nine sessions on Mack Creek. There were no captures during the last session on Pasture Creek.

Data from each stream were input to NOREMARK, a FORTRAN-based population

program (White 1996), and analyzed using a Lincoln-Peterson estimate. Programs such as Program Capture and Program Jolly were also tried, but the low number of recaptures on Pasture Creek made the results from these programs meaningless. NOREMARK, however, works well with low

recapture rates (J.P. Carroll, Warnell School of Forest Resources, University of Georgia, Athens,

GA, pers. comm.). These mark-recapture efforts yielded data on tailed frog densities, biomass, and

individual movements in both streams.

RESULTS

*Trophic ecology of *Ascaphus truei**

Aquatic food resources were consumed more frequently than terrestrial food resources by

the Mack Creek population of *Ascaphus truei* (Figure 1). Prey from both aquatic and terrestrial

sources was consumed by 20 tailed frogs whereas another 13 consumed only aquatic prey and only nine consumed only terrestrially derived food. Food items labeled “unidentifiable” were the sole

prey items found in the guts of three frogs and five frogs had empty stomachs. Thus, 50 frogs were

sampled and 45 had recently eaten. Of the 25 tailed frogs captured with only one food type present

in their guts, 12 had consumed aquatic larvae, one had eaten an emerged aquatic insect, five had

consumed arachnids, four had consumed other terrestrial prey, and three guts contained

unidentifiable parts. Figure 1 shows that aquatic larvae were present in more than half of all frogs but other prey types were not as ubiquitous. Predation on secondary consumers was common: tailed frogs consumed more spiders than any other terrestrial food resource, and predacious aquatic larvae such as *Callinectes* were extracted from the guts of five individuals. Frogs consumed prey items that crawled or landed in close proximity. One frog was observed consuming newly transformed adult trichopterans as they emerged from the water and were incapable of flight. Figure 2 shows that biomass from all aquatic food sources (aquatic larvae and emerged adults together) was about one third of all food sources consumed by an adult tailed frog. The biomass of aquatic insect larvae represented a ten-fold higher proportion of gut contents than aquatic emergence. Abundance of prey types failed to accurately reflect the biomass of prey types (Figure 3). For instance, emerged aquatic insects represented 19% of the total abundance (Figure 3) but only 3% of the total biomass (Figure 2) of prey types.

Intersite comparison

Abiotic factors: Mack and Pasture creeks were similar in their physical characteristics (Table 1); however, important differences also existed between the two streams. The area of the Pasture Creek watershed was approximately 81% of Mack Creek watershed, and the slightly lower stream discharge reported for Pasture Creek reflects this difference (Table 1). Pasture Creek was significantly warmer ($p < 0.05$) than Mack Creek, and it also had a different chemistry. Nitrate and ammonium concentrations were higher in Pasture Creek than in Mack Creek by factors of two and three, respectively (Table 1). However, the SRP concentration in Pasture Creek was half that found in Mack Creek.

Biotic factors: The biomass of aquatic food resources also differed in Mack and Pasture creeks. Epilithon and algae (chlorophyll-a) are both food resources for aquatic insect larvae and

larval frogs. Both were significantly lower in Pasture Creek than in Mack Creek ($p < 0.05$) (Table 2). Epithion biomass in Pasture Creek was roughly one half and chlorophyll was one third the value reported for Mack Creek. Invertebrate biomass was somewhat lower in Pasture Creek ($p < 0.10$). The densities and sex ratios of tailed frog populations also differed between streams. The tailed frog population along Mack Creek is larger than the population on Pasture Creek by a factor of three (Table 3). In each stream, the pool of individuals appeared to be completely marked because the population calculations yielded numbers with 95% confidence intervals that overlapped the number of individuals marked on each stream. Both the number of frogs marked and the calculated number of individuals per reach are reported, and the calculated values from the mark-recapture software were used to compute all derived values (e.g. density). Marked individuals were also used to derive sex ratios for each stream (Table 3). In Mack Creek, 37% of marked tailed frogs were male while 53% were male in Pasture Creek.

Mark-recapture studies also provided measurements of individual movement and biomass. A robust comparison between sites was not possible because of the low number of recaptures on Pasture Creek. Hence, I pooled these data because there was no detectable difference between streams (Table 3). The movements of individual tailed frogs in Mack and Pasture creeks show extreme fidelity to small stream segments. These two populations were highly philopatric. Individuals caught with more than three days between re-captures used only 3.8 ± 0.8 meters of the stream. The masses of individual frogs were also pooled since there was no significant difference in the average biomass of a frog between streams (Table 3). An average frog had a mass of 4.9 ± 0.2 g.

DISCUSSION

Trophic interactions of *Ascapbus truei*

This is the first study of *Ascapbus truei* presenting detailed data on the species' diet in terms of prey biomass. Past studies (e.g. Metter 1964) reported the gut contents of tailed frogs in terms of abundance of prey items found in the guts of dissected specimens and identified prey species to order. Species size may vary considerably within higher taxonomic divisions, and affect prey size, food quality, and handling time. Hence, it is inappropriate to only compare abundances of organisms found in the guts of geographically disjunct populations of predators. Figures 2 and 3 clearly show how particular types of prey may represent very different proportions of total prey biomass or abundance. Assessing prey importance by biomass ameliorates the problems inherent in measures of abundance. The size of the prey items becomes less important when results are presented as grams AFDM and comparisons of diets from geographically distinct and disjunct populations are more reliable. Metter (1964) reported no significant difference in the numbers of prey consumed by populations in Idaho and Washington, so he pooled the results from two geographically distant areas. Thus, his data must be viewed cautiously because there may have been significant differences in biomass of the prey items in each population that were not revealed by analyses of prey abundance.

Parker (1994) and Metter (1964) reported abundances of prey items in the guts of the Pacific giant salamanders and tailed frogs, respectively. The salamanders consumed prey almost exclusively from the stream during all seasons (Parker 1994), whereas tailed frogs in Idaho and Washington consumed large numbers of Trichoptera adults, Diptera adults, and spiders during July and August (Metter 1964). On the basis of numbers, Trichoptera adults are the most important food resource for tailed frogs in Idaho and Washington (Metter 1964). However, there is no indication as to which food resource constituted the most important energy pathway for the tailed frogs in Washington and

Idaho. Metter's data only reveal which prey type was consumed most often. On the other hand, biomass data from Mack Creek indicate that arachnids, other terrestrial food sources, and aquatic food sources were nearly equal in importance (Figure 2). Only using prey abundances in the analysis would have led to the same conclusions as previous investigators. My data show that in-stream sources of food account for 56% of the prey items found in the guts of 45 tailed frogs (Figure 3) while their biomass only represents 37% of the food consumed. Similarly, the abundance data provided by this study suggest that emerged aquatic insects are an important food resource for *Ascapbus truei* because they account for 19% of the tailed frogs' diet by abundance. However, the biomass data reveal that the abundance data may overestimate the importance of aquatic emergence because they only represent 3% of the biomass consumed by frogs during this study. Thus, these data show that tailed frogs are dependent on aquatic sources of food for energy and apparently devote considerable effort to obtaining aquatic prey, but the data also demonstrate the tailed frogs' strong reliance on food sources derived from the riparian zone.

Because food resources produced in the stream may be of great energetic importance to *Ascapbus truei*, events that alter stream habitats may affect tailed frog populations. The broad diet of tailed frogs (Metter 1964) does not imply that *Ascapbus truei* will readily switch to a diet more reliant on terrestrial food if aquatic food resources are reduced. Because tailed frogs require humid and cool habitats, the species may not be able to replace aquatic food with terrestrial food. Searching for enough terrestrial food to replace the 37% of its diet normally satisfied by aquatic food may require venturing into unsuitable dry, warm, or predator-rich environments.

Intersite comparison

Mack and Pasture creeks differ significantly in tailed frog population size and availability of their food resources and habitat. These differences are consistent with the types of changes

expected to result from the 1992 clear-cutting operations in Pasture Creek's watershed. The sex ratios for the tailed frog populations in Mack and Pasture creeks were also different, but within the range observed elsewhere. Only Metter (1964) has published sex ratios for *Ascaphus truei*; populations in Washington and Idaho were 37% and 50% male, respectively. The population on Mack Creek was 37% male and Pasture Creek was 53% male. These numbers match Metter's findings, and there is no evidence to link the difference in sex ratios to the timber management history in either watershed.

Population characteristics such as density can be explained by timber management histories in the Mack and Pasture creek watersheds. In 1957 Robert Storm captured and marked more than 80 tailed frogs in the same study reach on Pasture Creek (Joseph Beatty, Department of Zoology, Oregon State University, Corvallis, OR, personal communication); in 1998 I found 13. This difference represents an alarming six-fold decrease in the abundance of *Ascaphus*. Decreases in *Ascaphus* densities in intact forest stands downstream from logged areas have not been previously documented. In fact, Corn and Bury (1989) reported that "logging upstream from uncut forests also had no affect on the presence, density, or biomass of any species." However, declines in the tailed frog populations in streams traversing clear-cut areas are well-documented (e.g., Metter 1964, Bury 1968, 1988, Bury and Corn 1988, Corn and Bury 1989).

Tailed frogs are extremely sensitive to stream water temperature and can only tolerate narrow temperature ranges (e.g. Brown 1975, Claussen 1973a,b). Thus, the significantly higher ($p<0.05$) water temperature observed in Pasture Creek probably contributed to decreased tailed frog density. No researcher has reported finding *Ascaphus truei* in a stream warmer than 18° C, and abnormal development of tailed frogs may occur in streams nearing 15° C (Brown 1975). The range of temperatures observed in Pasture Creek is very close to this threshold. The highest nighttime temperature observed in Pasture Creek was 17° C, and temperatures were likely several degrees

higher during the day. In contrast, the highest nighttime temperature observed in Mack Creek was 15° C. Temperature is an excellent predictor of presence of tailed frogs; historically, no frogs were found in study sites with temperatures greater than 14.3° C (Welsh 1990), which is 0.5° below the average temperature in Pasture Creek.

The observed variations in *Asaphus truei* populations could also be the result of food limitation of larvae and adults. The tadpoles are filter feeders (Bury 1988) or scrapers (Pough et al. 1998) that feed on diatoms. Thus, *Asaphus truei* tadpoles in Pasture Creek could be food limited. The three-fold difference in algal (chlorophyll-a) biomass between Mack and Pasture creeks is similar to the three-fold difference in the tailed frog populations and suggests the possibility of a direct relationship between food supply and tadpole survival and growth.

The observed difference in algal (chlorophyll-a) biomass is the opposite of what I expected to find based on the observed water chemistry of both streams. The atomic N:P ratios were 4.1:1 and 14.8:1 in Mack and Pasture creeks respectively, suggesting N limitation in Mack Creek. Streams flowing over volcanic soils in the Cascades are often nitrogen limited (Munn and Meyer 1990), so the higher nitrogen concentrations in Pasture Creek suggest less nutrient limitation of the algae. It is possible that algal production was light limited in Pasture Creek, but canopy cover was similar in both study reaches. A likely explanation of the reduced algal biomass in Pasture Creek is scouring caused by sediment transport. Increased inputs of sediment are a documented effect of clear-cutting (Corn and Bury 1989), and I observed that Pasture Creek's stream bottom contained more fine particles than Mack Creek.

Another effect of sedimentation is reduced availability of interstices. Tailed frog adults and tadpoles use areas beneath rocks for refugia (e.g., Brown 1975, Metter 1964). Eggs are deposited beneath large rocks (Blaustein et al. 1995), adults winter beneath rocks (Daugherty and Sheldon 1982), and both adults and tadpoles use rocks for day time refugia (Metter 1964). Thus,

reproduction may be limited by a lack of suitable sites for depositing eggs or increased exposure to predation. There are no reports of egg predation in the literature, but predation by salamanders and snakes on tadpoles and adults is common (e.g., Bury 1988). A lack of refugia may expose both to increased predation by diurnal snakes. Salamanders such as *Dicamptodon tenebrosus* are nocturnal feeders as are *Ascapbus*. Thus, the availability of refugia is less of an issue than increases in *Dicamptodon* densities that have been reported following clear-cutting adjacent to streams (Sloat 1995). It is unclear whether such increases have been observed in undisturbed stream reaches downstream from clear-cuts.

Adult *Ascapbus truei* may also be food limited. The aquatic invertebrate biomass in Pasture Creek was somewhat smaller than in Mack Creek. There may be differences in relative abundance of food types, but that is unknown. Although Trichoptera adults were the most numerous food type in the guts of tailed frogs in Washington and Idaho (Metter 1964), the same may not be true in Mack and Pasture creeks because those analyses were only done once and could have coincided with a mass emergence of trichopterans. I observed tailed frogs consuming adult aquatic insects as they emerged from streams and mass emergences of various taxa during my study. Point surveys of a species that is such a highly opportunistic feeder on a highly variable resource may result in skewed data sets. Several sampling dates are necessary to compensate for this effect.

These differences between streams - less algal and epilithon biomass, less aquatic invertebrate biomass, warmer water temperature, more sedimentation, and fewer tailed frogs - are consistent with the differences in timber management practices in the two watersheds. Similar differences in water chemistry have been observed in other clear-cuts (e.g., Likens et al. 1970) as have differences in temperature (e.g., Brown and Krygier 1970). All are similar to what Bury and Corn (1988) suggest as long-term effects of logging on a stream ecosystem.

Mack and Pasture creeks are very different streams in terms of the biota they support.

Identifying the cause of these differences and their impact on *Asaphus truei* and other amphibian populations is an important topic for future research in the Pacific Northwest. The dependence of *Asaphus truei* on aquatic food resources indicates that the species may be an important component of riparian food webs. The transfer of energy (carbon) and nutrients between the stream and riparian zone should be understood so that responsible management can occur. Moreover, the stated goal of understanding the dynamics of and preserving biodiversity in the Pacific Northwest (Cissel et al. 1997) can only be reached by understanding how streams and riparian zones are both affected and impacted by the activities of species like *Asaphus truei*.

This study has demonstrated that that population size of tailed frogs varies between watersheds, arguably as a result of timber management histories. In light of the potential importance of these amphibians within riparian ecosystems, we need to know more about the energetic and nutrient-cycling functions of sensitive amphibian species and the system-wide consequences of their decline. If logging is a cause of their disappearance, then we need to find ways to protect these species from its far-reaching effects.

BIBLIOGRAPHY

- Allan, J.D. 1995. Stream Ecology. Chapman and Hall, London.
- Blaustein, A.R., J.J. Beatty, D.H. Olson, and R.M. Storm. 1995. The biology of amphibians and reptiles in old-growth forests in the Pacific Northwest. Gen. Tech. Rep. PNW-GTR-337. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Brown, G.W. and J.T. Krygier. 1970. Effects of clear-cutting on stream temperature. Water Resources Research 6(4):1133-1139.
- Brown, H.A. 1975. Temperature and development of the tailed frog, *Ascaphus truei*. Comparative Biochemistry and Physiology 50A:397-405.
- Bunnell, F.L. 1995. Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia: patterns and implications for conservation. Conservation Biology 9:636-644.
- Burton, T.M. and G.E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia 1975(3):541-546.
- Bury, R.B. 1968. The distribution of *Ascaphus truei* in California. Herpetologica 24:39-46.
- Bury, R.B. 1988. Habitat relationships and ecological importance of amphibians and reptiles. Pages 61-76 in K.J. Raedeke, editor. Streamside Management: Riparian Wildlife and Forestry Interactions. College of Forest Resources, University of Washington, Seattle, Washington.
- Bury, R.B. and P.S. Corn. 1988. Responses of aquatic and streamside amphibians to timber harvest: a review. Pages 165-181 in K.J. Raedeke, editor. Streamside Management: Riparian Wildlife and Forestry Interactions. College of Forest Resources, University of Washington, Seattle, Washington.

- Cissel, J.H. et al. 1998. A landscape plan based on historical fire regimes for a managed forest ecosystem: the Augusta Creek study. Gen. Tech. Rep. PNW-GTR-422. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 82p.
- Claassen, D.L. 1973a. The thermal relations of the tailed frog, *Ascaphus truei*, and the Pacific tree frog, *Hyla regilla*. Comparative Biochemistry and Physiology 44A:137-153.
- Claassen, D.L. 1973b. The water relations of the tailed frog, *Ascaphus truei*, and the Pacific tree frog, *Hyla regilla*. Comparative Biochemistry and Physiology 44A:155-171.
- Cole, E.C. W.C. McComb, M. Newton, C.L. Chambers, and J.P. Leeming. 1997. Response of amphibians to clear-cutting, burning, and glyphosate application in the Oregon Coast Range. Journal of Wildlife Management 61(3):656-664.
- Corn, P.S. and R.B. Bury. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. Forest Ecology and Management 29:39-57.
- Daugherty, C.H. and A.L. Sheldon. 1982a. Age determination, growth, and life history of a Montana population of the tailed frog, *Ascaphus truei*. Herpetologica 38(4):461-468.
- Daugherty, C.H. and A.L. Sheldon. 1982b. Age-specific movement patterns of the frog *Ascaphus truei*. Herpetologica 38(4):468-474.
- Davic, R.D. 1991. Ontogenetic shift in diet of *Desmognathus quadramaculatus*. Journal of Herpetology 25:108-111.
- Gomez D.M. and R.G. Anthony. 1996. Amphibian and reptile abundance in riparian and upslope areas of 5 forest types in western Oregon. Northwest Science 70:109-119.
- Hauer, F.R. and G.A. Lambert. 1996. Methods in Stream Ecology. Academic Press, Inc., San Diego, CA.

- Hawkins, C.P., M.L. Murphy, and N.H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* 63(6):1840-1856.
- Hawkins, C.P., M.L. Murphy, N.H. Anderson, and M.A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Canadian Journal of Fisheries and Aquatic Sciences* 40(8):1173-1185.
- Heyer, W.R. et al. 1994. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C.
- Horne, A.J. and C.R. Goldman. 1994. *Limnology*. McGraw Hill, Inc., New York, NY.
- Lambert, G.A., S.V. Gregory, C.P. Hawkins, R.C. Wildman, L.R. Ashkenas, and D.M. Denicola. 1992. Plant-herbivore interactions in streams near Mount St. Helens. *Freshwater Biology* 27:237-247.
- Likens, G.E., F.H. Bormann, N.M. Johnson, D.W. Fisher, and R.S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecological Monographs* 40:23-47.
- Metter, D.E. 1964. A morphological and ecological comparison of two populations of the tailed frog, *Ascaphus truei* Stejneger. *Copeia* 1964:181-195.
- Munn, N.L. and J.L. Meyer. 1990. Habitat specific solute retention in two small streams: an intersite comparison. *Ecology* 71:2069-2082.
- Murphy, M.L. and J.D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38:137-145.

- Noble, G.K. and P.G. Putnam. 1931. Observations on the life history of *Ascaphus truei* Stejneger. Copeia 1931(3):97-101.
- Nussbaum, R.A., E.D. Brodie, and R.M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. The University Press of Idaho, Moscow, Idaho.
- Parker, M.S. 1994. Feeding ecology of stream-dwelling pacific giant salamander larvae (*Dicamptodon tenebrosus*). Copeia 1994:705-718.
- Pough, H.F., R.M. Andrews, J.E. Cadle, M.L. Crump, A.H. Savitzky, and K.D. Wells. 1998. Herpetology. Prentice Hall, Upper Saddle River, NJ.
- Sloat, M. 1995. Population structure and feeding ecology of stream dwelling *Dicamptodon tenebrosus* in old-growth and regenerating clear-cut stretches of a Cascade Mountains stream. National Science Foundation Research Experience for Undergraduates (REU) Program at H.J. Andrews Experimental Forest. Unpublished.
- Smith, J.P., R.E. Gresswell, and J.P. Hayes. 1997. A research problem analysis in support of the Cooperative Forest Ecosystem Research (CFER) Program. Report to forest and Rangeland Ecosystem Science Center, Biological Resources Division, U.S. Geological Survey, Corvallis, Oregon. Oregon State University, Corvallis, Oregon. Oregon State University Contract Agreement No. H952A1-0101-25. 92p.
- Steinman, A.D. and G.A. Lambert. 1996. Biomass and pigments of benthic algae. Pages 295-313 in F.A. Hauer and G.A. Lambert, editors. Methods in Stream Ecology. Academic Press, Inc., San Diego, CA.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47(4):893-901.
- De Vlamming, V.L. and R.B. Bury. 1970. Thermal selection in tadpoles of the tailed frog, *Ascaphus truei*. Journal of Herpetology 4:179-189.

Welsh, H.H. 1990. Relictual amphibians and old-growth forests. *Conservation Biology* 4(3):309-

319.

Welsh, H.H. and L.M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. *Ecological Applications* 8(4):1118-1132.

Wetzel, R.G. and G.E. Likens. 1991. *Limnological Analyses*, second edition. Springer-Verlag, New York, NY.

White, G.C. 1996. Program NOREMARK Software Reference Manual. Department of Fisheries & Wildlife, Colorado State University, Fort Collins, CO.

Zug, G.R. 1993. *Herpetology*. Academic Press, San Diego, CA.

Table 1: Selected abiotic features of Mack and Pasture creek watersheds during August 1998. Reported discharges were recorded during the first mark-recapture collection period on each stream, and temperatures were recorded after sunset during collection periods. Values are means $\pm$ standard error (number of samples). Asterisks indicate the two streams are significantly different ($p < 0.05$).

	Mack Creek	Pasture Creek
Drainage area (ha)	580	472
Discharge (L/s)	65	60
Range H ₂ O Temp (°C)	12.0 – 15.0	13.0 – 17.0
Average H ₂ O Temp (°C)	13.8 $\pm$ 0.2 (14)	14.9 $\pm$ 0.4 (9)
NO ₃ ⁻ -N (µg/L)	54.4 $\pm$ 0.7 (8)	95.6 $\pm$ 0.5 (4)
NH ₄ ⁺ -N (µg/L)	3.6 $\pm$ 1.0 (8)	10.0 $\pm$ 0.0 (4)
SRP (µg/L)	13.9 $\pm$ 0.5 (8)	7.1 $\pm$ 0.4 (4)

Table 2. Comparison of food resources for tailed frog adults and larvae in Mack and Pasture creeks during August 1998. Values are means $\pm$ standard error and (n) represents the number of samples. Asterisks indicate the two streams are significantly different (** p<0.05, * p<0.10).

	Mack Creek		Pasture Creek
Epilithon (g AFDM/m ²)	2.990 $\pm$ 0.452 (11)	**	1.550 $\pm$ 0.218 (11)
Chlorophyll-a (g/m ²)	7.293 $\pm$ 1.127 (11)	**	2.493 $\pm$ 0.771 (11)
Invertebrates (g AFDM/m ²)	0.541 $\pm$ 0.214 (10)	*	0.402 $\pm$ 0.237 (10)

Table 3: Summary of mark-recapture data for tailed frogs collected on Mack and Pasture creeks during July and August 1998. Values are calculated values $\pm$ 95% confidence interval.

	Mack Creek	Pasture Creek
Frogs marked	41	13
Frogs (ind/50 m reach)	39 $\pm$ 2	13 $\pm$ 1
Sex ratio (m:f, % male)	0.58 : 1, 37%	1.16 : 1, 53%
Frog density (ind/m)	0.78 $\pm$ 0.02	0.26 $\pm$ 0.01
Frog biomass (g/ind)	4.75 $\pm$ 0.18	5.55 $\pm$ 0.50
Frog biomass (g/m)	3.71 $\pm$ 0.24	1.44 $\pm$ 0.10
Ave. range of individuals (m)	4.0 $\pm$ 0.9	2.5 $\pm$ 1.5

Figure 1: Frequency of occurrence of prey types in the guts of 50 tailed frogs (*Ascaphus truei*) from Mack Creek during August 1998. Bars represent fraction of tailed frog population that consumed a given prey type. Guts of 50 tailed frogs were flushed; five had not consumed any food.

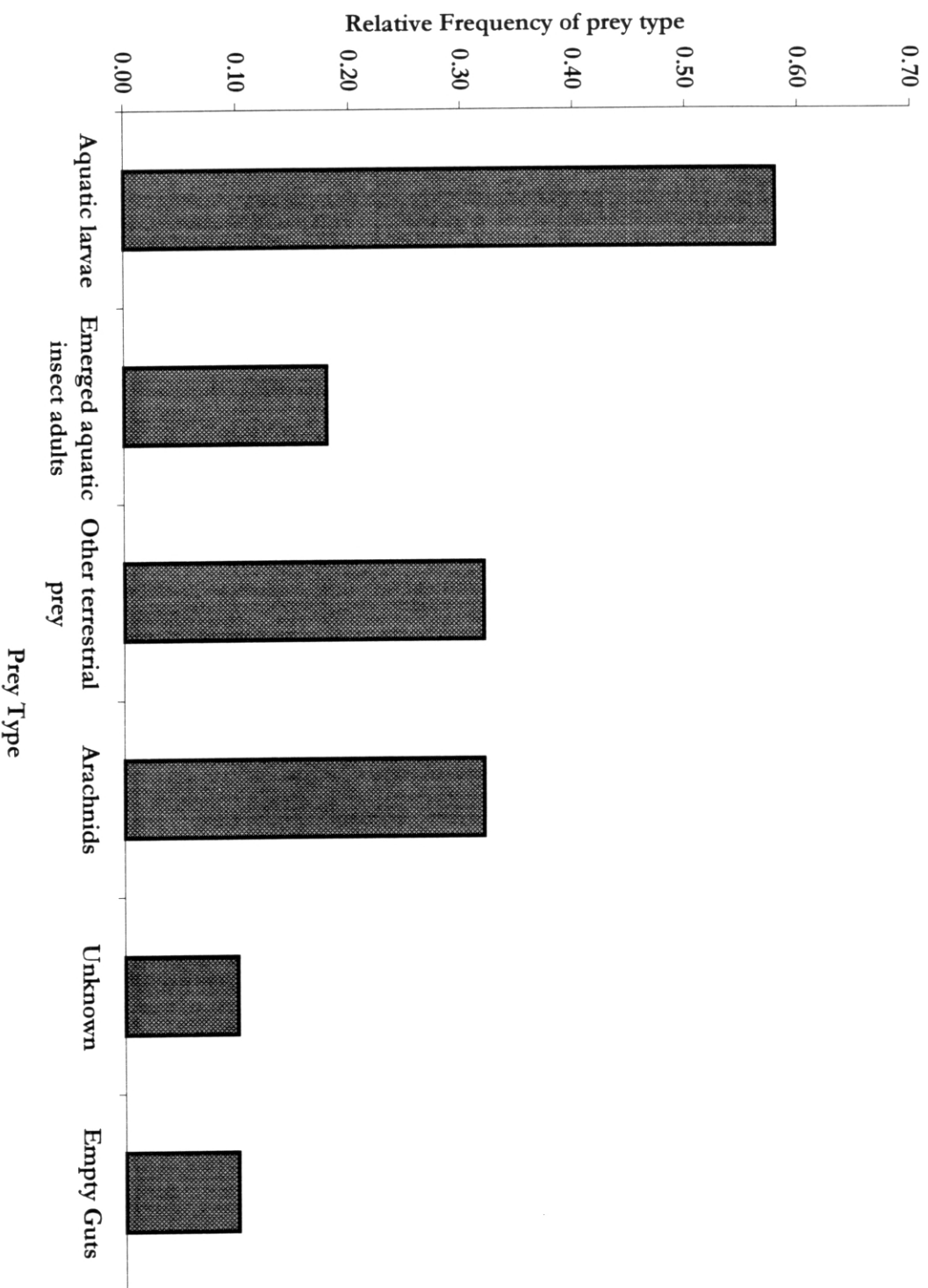


Figure 2: Percentages of total biomass of prey types found in the guts of 45 tailed frogs (*Ascaphus truei*) from Mack Creek, OR during August 1998. The total biomass of all food items was 346.7 mg AFDM, and the average biomass of prey items in individual tailed frogs was 7.7 ± 2.3 mg AFDM.

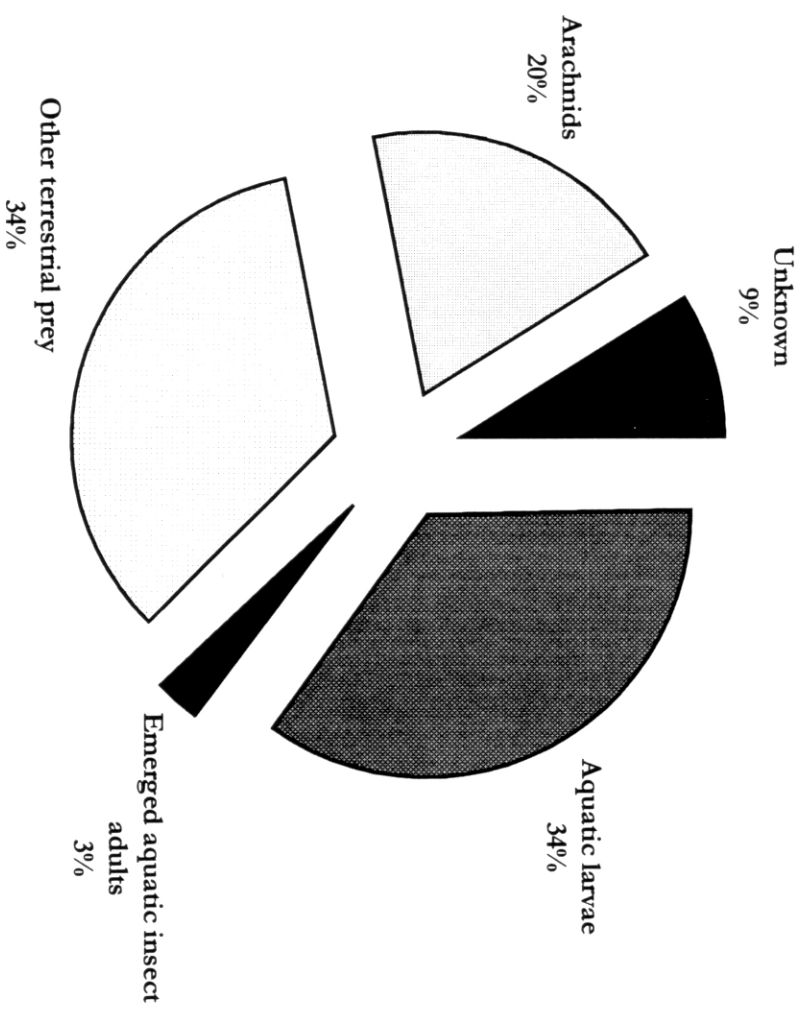


Figure 3: Percentages of total abundance of prey types found in the guts of 45 tailed frogs (*Ascaphus truei*) from Mack Creek, OR during August 1998. 120 food items were found in the guts of 50 tailed frogs and values ranged from 0-18 food items.

