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Feeding Niches of Forest Salamanders: Indirect Effects of Gypsy Moth Pesticides on Prey Selection and Potential Overlap Between Adults of Six Species

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Dr. Leonard J. Deutsch

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Abstract

Amphibian declines and deformities are indictors of pollution and other environmental impacts. Pesticides, such as *Bacillus thuringiensis* var. *kurstaki* (*Bt*), may produce non-target effects on salamanders by impacting their food supply, ultimately resulting in population declines. Salamanders were used as an assessment tool of pesticide impacts before populations decline. Diet analysis determined if *Bt* affected food consumption of two salamander species (*Desmognathus ochrophaeus* and *P. cinereus*). Nine plots in the Monongahela National Forest, West Virginia were used in this study. Three plots were sprayed with *Bt* in 1997 and 1998, three were sprayed with a gypsy moth specific insecticide (Gypchek®) in the same years, and three received no pesticide application. Stomach contents were obtained by hand-collection and stomach pumping specimens in 1997 and 1998. Food items were compared between treatments in 1997 and 1998 separately, and for both years combined. Salamanders were also obtained by pitfall traps from 1995 - 1997. Stomach contents from these samples were compared before and after application of each treatment. There were no differences in diet of either species between treatments after pesticide application in either 1997 or 1998 (Spearman rank correlation, p=0.05). There was no correlation in the diet of either species before and after application of *Bt* or plots with no pesticide application. There was a correlation of *D. ochrophaeus* diets from Gypchek plots before and after application. Based on the diets of hand collected salamanders compared between treatments, there is no evidence to show that *Bt* affects salamander foraging.

Stomach contents, habitat, daily activity and monthly activity determined feeding niche overlaps among six species (*D. fuscus, D. monticola, D. ochrophaeus, P. cinereus, P. glutinosus, P. hoffmani*). I made 15 pairwise comparisons representing all possible combinations. There are 5 feeding niche overlaps based on food and habitat (Spearman rank, p=0.05). Competition for food may be reduced between *P. cinereus* and *P. glutinosus* and between *D. fuscus* and *D monticola* by differences in daily activity. Different monthly activity may reduce competition between *P. cinereus* and *P. hoffmani. Desmognathus ochrophaeus* is a semi-aquatic species with feeding niche overlaps with both *D. fuscus* and *P. cinereus*. Diets from these six species show a continuum of food items from terrestrial to aquatic habitats.

Introduction

Salamanders are a vital part of the food web in forest and stream communities. They feed primarily on invertebrates and are the top predators of many first- and second-order streams, as well as secondary consumers in leaf litter habitats. Sixty percent of the energy which passes to birds and mammals passes through salamanders (Burton and Liken, 1975). Their role as both predator and prey make them a crucial link between insects and other vertebrates.

A great reduction in the abundance of primary producers (plants) or primary consumers (herbivores) will affect higher consumers by a cascade effect (Townsend, 1996). Since salamanders link insects and other vertebrates, disturbances in the insect community can be detected by changes in salamander diets before the disturbance affects the whole ecosystem.

Widespread use of pesticides is one disturbance that could change an ecosystem by reducing insect abundance. *Bacillus thuringiensis* var. *kurstaki* (*Bt*) is a broad spectrum pesticide which interferes with insect feeding (Reardon et al., 1994; Reardon and Wagner, 1995). Several studies have shown decreased abundance of non-target lepidopteran larvae due to *Bt* applications and suggest that large scale *Bt* treatments may alter the abundance of other non-target insects (Hilbeck et al., 1998; Miller, 1990; Sample et al., 1996; Wagner et al., 1996). Although 4.2 million acres of land have been sprayed by *Bt* since 1980, long-term studies of *Bt* effects on non-target animals are lacking (Reardon et al., 1994; Reardon and Wagner, 1995).

Studies have shown that a reduction of prey items as a result of *Bt* adversely impacts insectivores. Rodenhouse and Holmes (1992) found a reduction in nests, fledgings per nest and nestling growth rates and survival of the black-throat blue warbler following application of *Bt.* In another study, masked shrews emigrated from treatment plots or shifted food resources as a direct effect of decreased abundance of lepidopteran larvae (Bellocq et al., 1992).

To test potential impacts on forest systems from *Bt* applications and gypsy moth (*Lymantria dispar*) defoliation, the USDA-Forest Service is funding a long-term project in the Monongahela (MNF) and George Washington National Forests (West Virginia and Virginia, respectively). This project has focused on birds, salamanders and non-target insects since 1995 and will continue through the year 2000.

Bacillus thuringiensis was sprayed on three 200 hectare plots in the MNF in 1997 and 1998. Two years of pre-treatment data (1995 & 1996) were collected and two post-treatment years will follow the 1998 application. In this thesis, I investigate potential alterations of salamander diets as a result of *Bt* applications. I hypothesize that *Bt* will not alter the diets of two forest salamanders, *Desmognathus ochrophaeus* and *Plethodon cinereus.* I predict no alteration of diet since forest salamanders are euryphagous and do not rely on one insect type for food.

I also examined the diets of six salamander species to determine feeding niche overlaps. Consumption of similar food items may place salamanders in competition; however, staggered feeding schedules or non-overlapping habitats may reduce competition. For example, *Plethodon cinereus* and *P. hoffmani* were found to prey on the same food; however, they foraged at different times of the day, reducing the level of competition (Fraser, 1976).

Competition for food between two salamander species has been thoroughly studied (Canterbury and Pauley, 1990; Fraser, 1976; Townsend and Jaeger, 1998; Marcum, 1994; Petranka, 1984). However, limited work has been done comparing multiple salamanders in a forest. Burton (1976) found five species of plethodontid salamanders preyed on similar prey taxa but consumed different prey sizes, reducing potential competition. Prey taxa, prey size, habitat and time of day foraging occurs need to be identified to adequately determine feeding niche overlaps between salamander species. To examine the feeding niche overlaps between six species of forest salamanders (*Desmognathus fuscus, D. monticola, D. ochrophaeus, Plethodon cinereus, P. glutinosus,* and *P. hoffmani*), 15 hypotheses comparing species pairs in all possible combinations (*D. fuscus* vs *D. monticola*, *D. fuscus* vs *D. ochrophaeus*, etc.) will be tested. They are:

Based on prey taxa, prey size, habitat and time of day foraging occurs...

(1) *D. fuscus* will not have a feeding niche overlap with *D. monticola.*

(2) *D. fuscus* will not have a feeding niche overlap with *D. ochrophaeus.*

(3) *D. fuscus* will not have a feeding niche overlap with *P. cinereus.*

(4) *D. fuscus* will not have a feeding niche overlap with *P. glutinosus.*

(5) *D. fuscus* will not have a feeding niche overlap with *P. hoffmani.*

(6) *D. monticola* will not have a feeding niche overlap with *D. ochrophaeus.*

(7) *D. monticola* will not have a feeding niche overlap with *P. cinereus.*

(8) *D. monticola* will not have a feeding niche overlap with *P. glutinosus.*

(9) *D. monticola* will not have a feeding niche overlap with *P. hoffmani.*

(10) *D. ochrophaeus* will not have a feeding niche overlap with *P. cinereus.*

(11) *D. ochrophaeus* will not have a feeding niche overlap with *P. glutinosus.*

(12) *D. ochrophaeus* will not have a feeding niche overlap with *P. hoffmani.*

(13) *P. cinereus* will not have a feeding niche overlap with *P. glutinosus.*

(14) *P. cinereus* will not have a feeding niche overlap with *P. hoffmani.*

(15) *P. glutinosus* will not have a feeding niche overlap with *P. hoffmani.*

This set of hypotheses will identify feeding niche overlaps between the most abundant salamanders on the study plots in the Monongahela National Forest, West Virginia.

Long-term Gypsy Moth Project

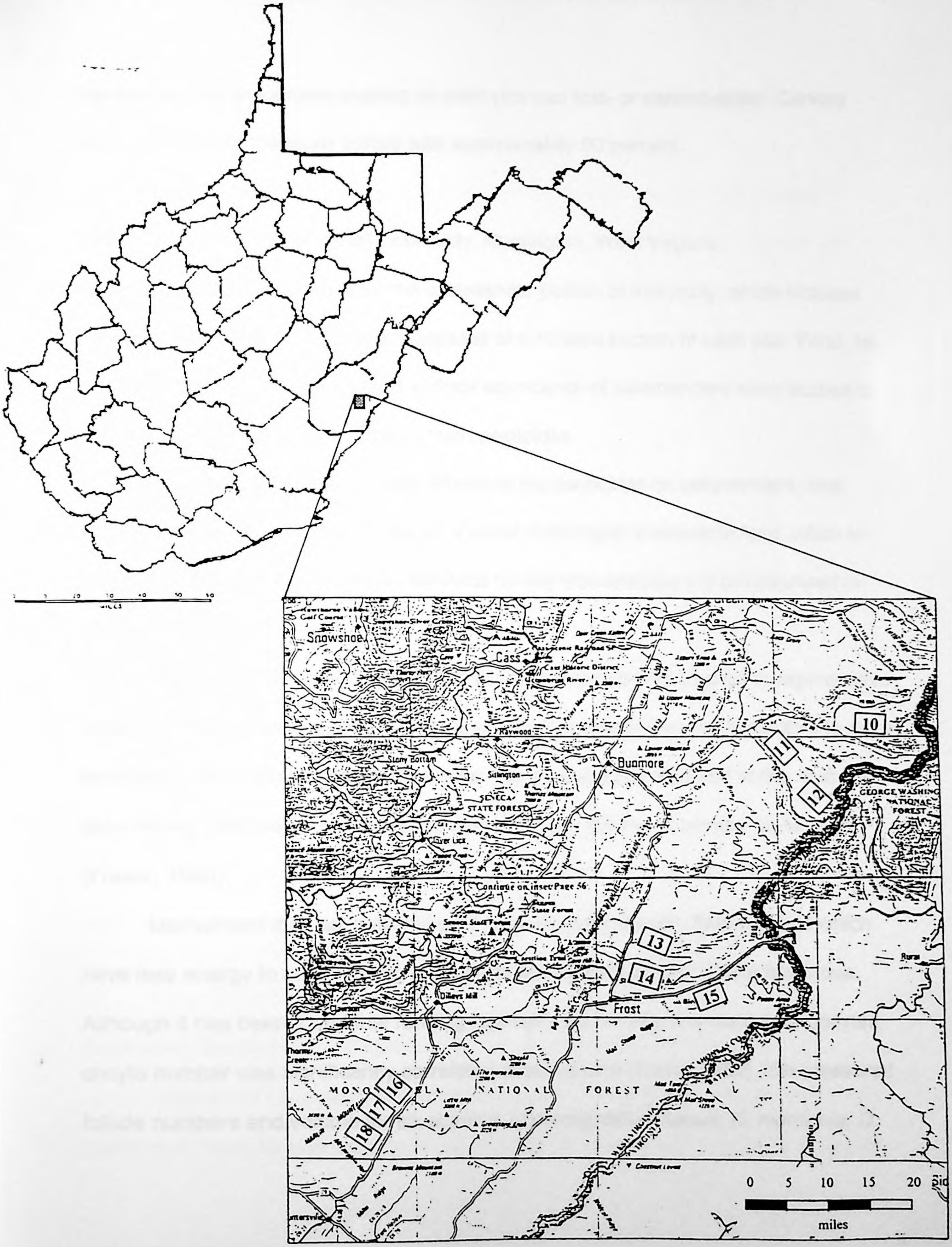
Background and Site Description

The long-term gypsy moth (LTGM) project, funded by the USDA-Forest Service. began in 1995 to test indirect impacts of gypsy moth defoliation and non-target pesticides on forest ecosystems. Three treatments were examined: *Bacillus thuringiensis* var. *kurstaki* (*Bt*), no pesticide treatment (defoliation), and Gypchek. Gypchek is a species-specific pesticide which induces a viral infection within gypsy moth larvae. This pesticide infects only the target insect, and has no adverse impact on other arthropod species or vegetation (Reardon and Podgwaite,1992). Due to its benign impacts on forests and its elimination of gypsy moth defoliation, Gypchek plots were established as positive controls.

During the first two years, baseline data were collected on all plots for salamanders, birds and arthropods. Gypchek and *Bt* were sprayed in 1997 and 1998 in the Monongahela and George Washington National Forests. Post-treatment data will be collected through the year 2000.

Eighteen 200 hectare plots, representing six replicates of each treatment, were established. Plots 1-9 were established in the George Washington National Forest, Augusta County, VA. These plots were not used in the salamander portion of the study, so will not be discussed further. Plots10-18 were designated in the Monongahela National Forest, Pocahontas County, WV and are shown in Fig. 1. Plots 11, 15, and 18 were sprayed with *Bt*. Gypchek was sprayed on 10, 13 and 17 and plots 12, 14 and 16 had no pesticide application. Vegetation on all sites is predominately mixed

Figure 1. Location of LTGM plots 10-18 in the Monongahela National Forest, Pocahontas County, WV.


MILES
Snowshoe
Cass
Stony Bottom
Sitlington
Dunmore
SENECA STATE FOREST
Clover Lick
Continue on inset Page 56
Seneca State Forest
Dilleys Mill
Frost
MONONGAHELA NATIONAL FOREST
GEORGE WASHINGTON NATIONAL FOREST
10
11
12
13
14
15
16
17
18
0 5 10 15 20
miles

hardwoods and the stream studied on each plot was first- or second-order. Canopy cover throughout the study period was approximately 90 percent.

Salamander Studies Marshall University, Huntington, West Virginia.

The study areas used for the salamander portion of this study, which includes the work described in this thesis, consisted of a 10 acre section of each plot. Food, fat stores, reproductive potential and surface abundance of salamanders were studied to determine indirect impacts of gypsy moth pesticides.

Assuming there are no direct effects of the pesticides on salamanders, one potential impact is a change in diet as a result of changes in available food, which is described throughout this thesis. Methods for the food analysis will be discussed in detail in the following section.

Inadequate diet may be amplified in salamanders by reduced fat or reproductive potential. If salamanders are not acquiring proper nutrients, they will be unable to store fat needed to aestivate through the winter. Fat stores were measured in this study by determining lean weight in the first 18 mm of the tail, the site of primary fat storage (Fraser, 1980).

Malnutrition may adversely impact reproductive potential. Salamanders which have less energy to invest in egg production will produce smaller and/or fewer ova. Although it has been found that feeding regimens did not alter the number of oocytes, oocyte number was significantly correlated to tail volume (Fraser,1980). We measured follicle numbers and volume for six species (*Desmognathus fuscus, D. monticola, D.*

ochrophaeus, Plethodon cinereus, P. glutinosus and *P. hoffmani*) to determine if reproductive potential was inhibited by either treatment.

Decreased fat stores, reproductive potential or both may ultimately result in decreased survival of salamander populations, which can be measured as surface abundance. Surface abundance of salamanders is also reduced by environmental factors such as increased soil temperature, decreased soil moisture and relative humidity, and decreased leaf litter, which are characteristic impacts of clearcutting and defoliation.

A mark-recapture study was conducted within the study area to determine if salamander surface abundance was impacted by either *Bt* applications or gypsy moth defoliation. We examined five transects: three 100 meter terrestrial and two 50 meter aquatic. The first terrestrial transect consisted of 10 coverboard sites and the second contained 10 point surveys, in which leaf litter was searched for salamanders. The final terrestrial transect was searched at night by 2-3 investigators. The day aquatic transect consisted of 10 juvenile refugia bags and 10 numbered flat rocks. The second aquatic transect was searched at night.

Results of diet, tail fat, reproductive potential and surface abundance for each species were compared between treatments and between pre- and post-treatment years.

Arthropod Studies West Virginia University, Morgantown, West Virginia

Arthropods were sampled in the 30-ha core of each plot by blacklight trapping, banding of trees, foliage pruning, Malaise trapping and pitfall trapping. The sampling period was from early May to mid-August each year of the project. Multivariate analysis was used to determine spatial and temporal changes in arthropod communities in control and treatment plots.

In addition to selected arthropods used for this portion of the LTGM study (Hymenoptera, Diptera, Coleoptera), taxa known to compose a high percentage of salamander and bird diets were also identified to family, genus or species (Diplopoda, Formicidae, certain Diptera and Coleoptera). This information will be used in diet analysis of both salamanders and birds.

Bird Studies University of Georgia, Athens, Georgia

The objectives of this portion of the LTGM study were to determine if vegetation characteristics, bird abundance and bird productivity differ as a result of *Bt* applications or defoliation. Data were collected from six parallel 600m transects separated by 100m on each plot. Twenty-eight random points were established for vegetation analysis. Selected trees were monitored for defoliation throughout the study.

Bird abundance was estimated using point counts made at 50 randomly selected locations in each plot. All birds seen or heard in five minutes were tallied. Bird productivity was measured by searching for nests of selected bird species (red-eye vireos, solitary vireo, worm-eating warbler, wood thrush and ovenbird).

Data collected by each research team are being collaborated into a final analysis of the effects of *Bt* and gypsy moth defoliation on non-target arthropods, salamanders and birds. Vegetation, soil, weather and GPS data for all plots are shared by all research groups. Links between vegetation, insects, birds and salamanders are being made in a cooperative effort by West Virginia University, Marshall University and University of Georgia. This analysis provides a broad look at the effects of pesticide and defoliation on forest ecosystems.

Methods: Salamander Diet Analysis

Salamander collection

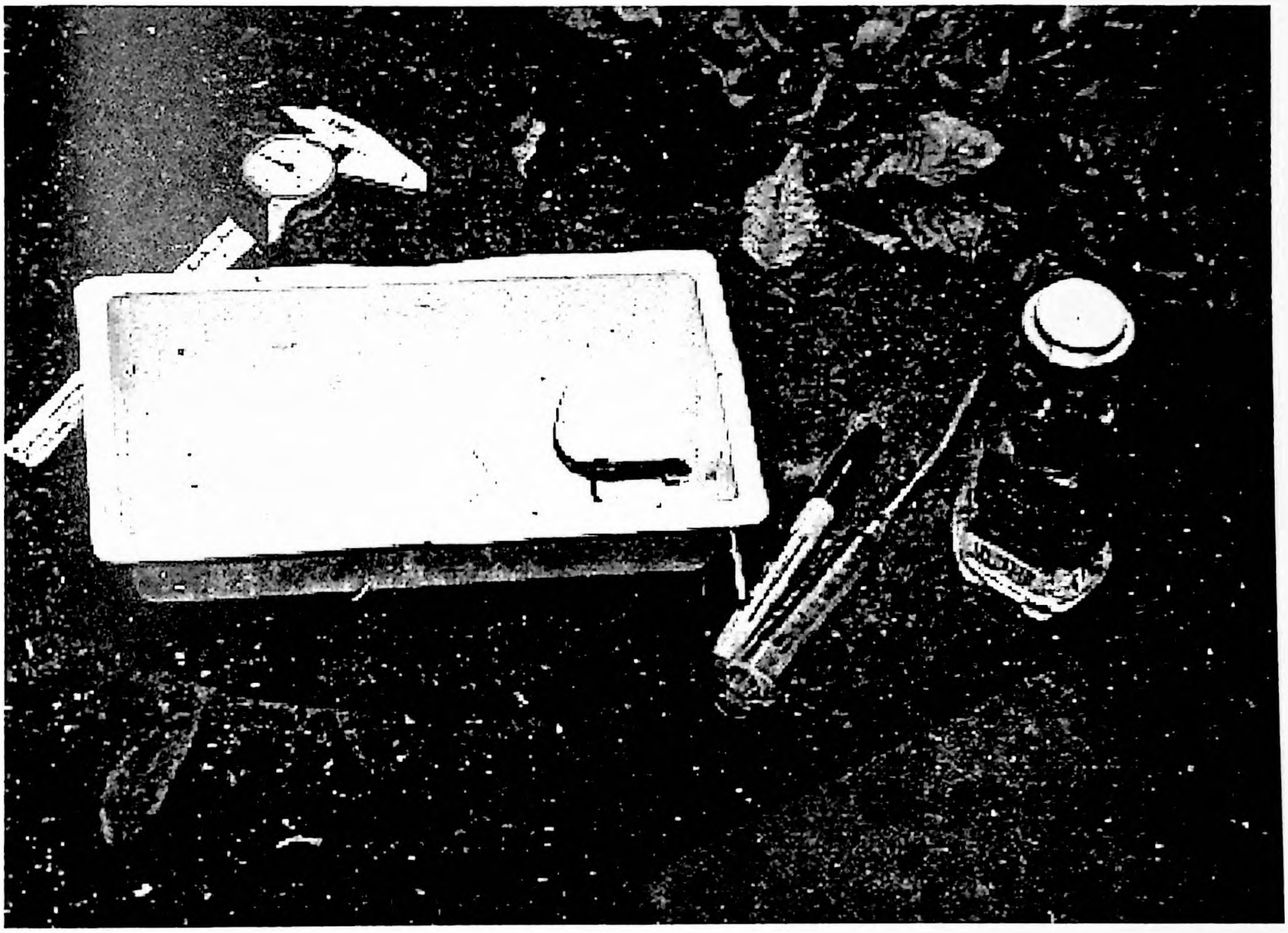
I studied six salamander species: three terrestrial (*P. cinereus, P. glutinosus* and *P. hoffmani*), two aquatic (*Desmognathus fuscus* and *D. monticola*) and one semi-aquatic (*D. ochrophaeus*). These species are the most common and abundant salamanders within the study area. Stomach contents were obtained by hand collection of salamanders, pitfall traps, and stomach pumping.

Hand collection of specimens was conducted from May-September 1997 and April-October 1998 by overturning cover objects in terrestrial and streamside habitats. Six adults of each species were taken per plot per month. Collected specimens were immediately placed in zip-lock bags in coolers with ice and taken back to the lab within 24 hours, frozen and placed in formalin.

Pitfall traps were placed throughout the forest as part of the insect portion of the LTGM study conducted by West Virginia University. Salamanders were initially preserved in propylene glycol in pitfalls and later placed in 70 percent ethanol. Pitfall samples were collected from May to Mid-August, 1995 - 1997.

The final method of obtaining salamander gut contents was stomach pumping. Salamanders were found throughout the study areas by overturning all possible cover objects. Stomachs were pumped in the field with a 10cc syringe fitted with 18 gauge rubber tubing (Fig. 2). Stomach contents were obtained and immediately placed into 70 percent ethanol. Salamanders were weighed, measured for snout-vent length (SVL) and cranial width (CW), toe clipped and returned to the original cover object. Time of day, cover object, soil, air and water (when applicable) temperature, and relative

Figure 2. Stomach pumping apparatus: syringe fitted with 18 gauge rubber tube. (Photo by Karen Raimondo)



[illegible]

humidity were measured where each salamander was found.

Hand collected and stomach pumped specimens were found at random locations with a conscious effort to sample the same number of each species throughout the study areas. Specimens obtained by these two methods were pooled and will be referred to from here on as "hand-collected" specimens.

All salamanders were measured for SVL and CW which were compared interspecifically by a one-way Analysis of Variance (ANOVA). Preserved specimens were placed in the West Virginia Biological Survey Museum, Marshall Univerisity, Huntington, West Virginia.

Identification of stomach contents

Stomach contents were identified to family when possible and to order when only remnants of the whole prey items were present. For example, an elytron of a beetle was identified to the order Coleoptera. When whole prey items were present, length and width were measured. Prey size, measured as volume, was calculated assuming the item as a cylinder (Burton,1976; Fraser, 1976). Invertebrate taxonomy follows Borror et al. (1992) and Merritt and Cummins (1996). Empty stomachs, plant material, rocks, and mostly-digested unidentifiable organic matter were not included in the analyses.

Data Analysis: prey size / prey taxa

For both the pesticide and feeding niche overlap studies, I compared prey taxa and prey size. In the prey taxa analysis, items were separated into broad taxonomic categories based on body forms (adult/larva/apterous) and general habit (flying, leaf litter, aquatic) (Table 1). The proportion of the total diet each prey taxon composed was calculated for each salamander species.

In the prey size analysis, 10 size categories representing prey volumes were established. Different approaches of calculating prey volume of vertebrates have been used. Vitt and Avila-Pires (1998) calculated all prey items as a prolate spheroid. However, millipedes and centipedes, which can compose up to 10% of terrestrial salamander diets, have long and slender bodies closely resembling a cylinder. Beetles and ants which can compose up to 50% of the diets of *P. cinereus* and *P. hoffmani*, although not as long as a centipede or millipede, have the general body shape of a cylinder (3.5 length:1.0 width). Fish diets have been calculated by using the volume of the most similar shape of the organism: cube, cylinder, rectangular parallelepiped, or sphere ($\mathrm{M^cComish}$, 1967). To remain consistent, I used the volume of a cylinder for all prey items. The proportion of total prey items to fall within each size range was determined for each salamander species (Fraser, 1976; Burton, 1976). Spearman rank correlation coefficients and Fisher's exact test (2-tail) statistically compare dietary overlap of both prey taxa and prey size analyses.

Insect parts (e.g., elytra and hemelytra), which were identifiable to order but could not be used to calculate total prey volume, were included in the prey taxa analysis but not in the prey size analysis. A linear regression of salamander CW and prey volumes was made to determine if there was a correlation between the sizes of predator and prey.

Table 1. A list of the broad taxonomic categories (arthropod classes, insect and salamander orders) and general habitat of the prey items used in the prey taxa analysis.

Broad taxonomic category	General habit
Acari	leaf litter
Araneae	leaf litter
Benthic invertebrates	aquatic (benthos)
Chilopoda/Diplopoda	leaf litter
Coleoptera (adult)	leaf litter
Collembola	leaf litter/aquatic
Decapoda	aquatic
Diptera (adult)	flying
Diptera (larvae)	leaf litter/aquatic
Homoptera/Hemiptera	leaf litter
Hymenoptera (Formicidae)	leaf litter
Hymenoptera (adult)	flying
Lepidoptera (adult)	flying
Lepidoptera (larvae)	leaf litter
Mecoptera	flying
Miscellaneous larvae	terrestrial/leaf litter
Orthoptera	leaf litter
Plecoptera	flying
Pseudoscorpionida	leaf litter
Gastropoda	leaf litter/aquatic
Salamander larvae	aquatic
Trichoptera	flying

Intraspecific comparisons: treatments

Only *P. cinereus* and *D. ochrophaeus* were used to determine changes in diet as a result of *Bt* applications and gypsy moth defoliation. Sample sizes of other species were not large enough to be compared statistically. Stomach contents were compared for *P. cinereus* and *D. ochrophaeus* between all treatments in post-treatment years. For example, the diets of *P. cinereus* from *Bt* plots were compared to *P. cinereus* from control plots.

Separate comparisons were made for pitfall and hand-collected specimens because pitfalls were placed in the same location every year. Therefore, there was consistency of pitfall sampling locations from year to year, whereas hand-collected specimens were found from random locations throughout the study site. Table 2 shows a list of comparisons made between treatments for each *P. cinereus* and *D. ochrophaeus*.

Intraspecific comparisons: pre- and post-treatment years

Diets of *P. cinereus* and *D. ochrophaeus* were compared between pre-treatment (1995 + 1996) and post-treatment (1997) years for each treatment. For example, the diet of *P. cinereus* from *Bt* plots before treatments were compared to those from the same plot after treatment (Table 3). These comparisons were made using pitfall samples only since there were no hand-collected samples prior to 1997.

Table 2. Intraspecific comparisons between treatments for *D. ochrophaeus* and *P. cinereus*. Each comparison was analyzed for overlaps of prey taxa and prey size.

Sample	Species	Treatment 1	Treatment 2
Handcollected	*D. ochrophaeus*	*Bt*	no treatment
	D. ochrophaeus	Gyp	no treatment
	D. ochrophaeus	*Bt*	Gyp
	P. cinereus	*Bt*	no treatment
	P. cinereus	Gyp	no treatment
	P. cinereus	*Bt*	Gyp
Pitfalls	*D. ochrophaeus*	*Bt*	no treatment
	D. ochrophaeus	Gyp	no treatment
	D. ochrophaeus	*Bt*	Gyp
	P. cinereus	*Bt*	no treatment
	P. cinereus	Gyp	no treatment
	P. cinereus	*Bt*	Gyp

Table 3. Comparisons of pre-treatment years (1995 + 1996) and post-treatment year (1997) for *D. ochrophaeus and P. cinereus*. Each comparison was analyzed for overlaps of prey taxa and prey size. Comparisons were made using pitfall specimens only.

Species	Variable 1	Variable 2	Treatment
D. ochrophaeus	Pre-treatment	Post-treatment	*Bt*
D. ochrophaeus	Pre-treatment	Post-treatment	Gyp
D. ochrophaeus	Pre-treatment	Post-treatment	no treatment
P. cinereus	Pre-treatment	Post-treatment	*Bt*
P. cinereus	Pre-treatment	Post-treatment	Gyp
P. cinereus	Pre-treatment	Post-treatment	no treatment

Insect Data

Data collected by West Virginia University were used to determine if insect abundance or diversity varied before and after treatment or between treatments after pesticide application. I focused on the results of Malaise and pitfall traps to collect data on ants, beetles and small flying insects, which are the primary components of salamander diets. I also concentrated on changes in larval lepidopterans, which are the most likely insects directly affected by *Bt* applications (Reardon et al., 1994) and compose 10 percent of the diet of *P. glutinosus.*

Interspecific comparisons: food overlap

I compared diets of hand-collected specimens from 1997 and 1998 to determine feeding niche overlaps between species. Pitfall samples were not included in these comparisons. Fifteen comparisons representing all possible combinations of species pairs were made. Spearman rank and Fisher's exact test compared prey taxa and size of each species pair.

Interspecific comparisons: habitat overlap

Three terrestrial and two aquatic transects were searched monthly in each study area as part of the salamander portion of the LTGM project. These investigations were conducted by two to three investigators since 1995. I incorporated these data into this project to determine habitat overlaps between species. Data presented here are from 1997 and 1998. These data are also used in the daily and monthly activity sections described in the following sections.

Three terrestrial transects spanned from ravine to ridge. One transect was monitored at night. Those examined during the day had coverboards and leaf litter searches. Aquatic transects were 50 meters in length. One was monitored during the day by shaking out refugia bags made of litter and rock in mesh bagging (Pauley and Little, 1998) and lifting 10 numbered flat rocks. The second was monitored at night by walking the transects and looking for salamanders that were on the surface of leaf litter and rocks. No cover objects were overturned during these searches.

Habitat breadth, an estimate of the range of different habitats a species occupies, was calculated for each species. I defined four different habitats: stream, terrestrial 0-50m from stream, 50-100 m from stream, and ridge. Habitat breadth was calculated by the formula (Schoener, 1970; Colwell and Futuyma, 1971; Krzysik, 1979; Kees 1994):

$$B'_i = -\Sigma N_{ij}/Y_i \log N_{ij}/Y_i$$

where N_{ij}= number of salamander species *i* found at habitat *j*, and Y_i = total number of species *i* found in all resource areas. Results are based on a scale of 0 to 1, with a value of 1 representing equal utilization of all habitats.

Habitat overlap, a percentage of habitats shared between two species, was measured for all species pairs from the equation (Holomuzki, 1980; Kees 1994):

$$\text{Overlap} = 1 - {}^1/_2\, \Sigma\, |N_{ij}/Y_i - N_{hj}/Y_h|$$

where N_{ij}=number of species *i* found at resource *j*, Y_i=total number of species *i* found in all resources, N_{hj}=number of species *h* found at resource *j*, and Y_h= total number of species *h* found in all resources.

Interspecific comparisons: daily activity overlap

The number of each species found during the day and at night was used to compare daily activity of species. Percentages were calculated to determine the frequency of each species found under cover objects during daytime investigations and on the surface of leaf litter and rocks at night.

Interspecific comparisons: monthly activity overlap

Although all salamander species were randomly collected throughout the field seasons (April-October, 1997-1998), we observed some species were more active in some months than others. For example, the majority of *P. hoffmani* were found during spring months and were not found from June through September. Based on these observations, I used the number of each species found in each month as an estimate of monthly activity throughout the year.

Predator-prey size relationship

I used linear regression to identify a correlation between salamander size and the largest prey item found in each diet. Regression was made using LOG_{10} cranial width and LOG_{10}prey volume. Cranial width was used as the morphometric parameter which limits the size of prey a salamander can eat.

Environmental parameters

Environmental parameters important to salamander activity, abundance and survival are air and soil temperature, relative humidity, soil moisture, soil pH, and leaf litter mass and moisture. These parameters were measured monthly for each plot. One way ANOVA determined if mean environmental data varied between treatment plots and on a monthly basis.

Statistical analysis

All statistical analyses except Fisher's exact test were performed by SigmaStat®. Fisher's exact test was performed using SAS Canonical Discriminant Analyses. All graphs and Fig.s were completed using Microsoft® Excel version 7.0.

Salamander Life Histories

Desmognathus fuscus (Green) (northern dusky) is a robust salamander inhabiting streamside habitats. Its coloration is usually brown or gray with a light stripe down the back bordered by wavy or scalloped margins (Fig. 3). These physical characteristics are extremely variable. Its average total length is 12.7 cm and its tail is moderately keeled. There are 14 costal grooves (Green and Pauley, 1987).

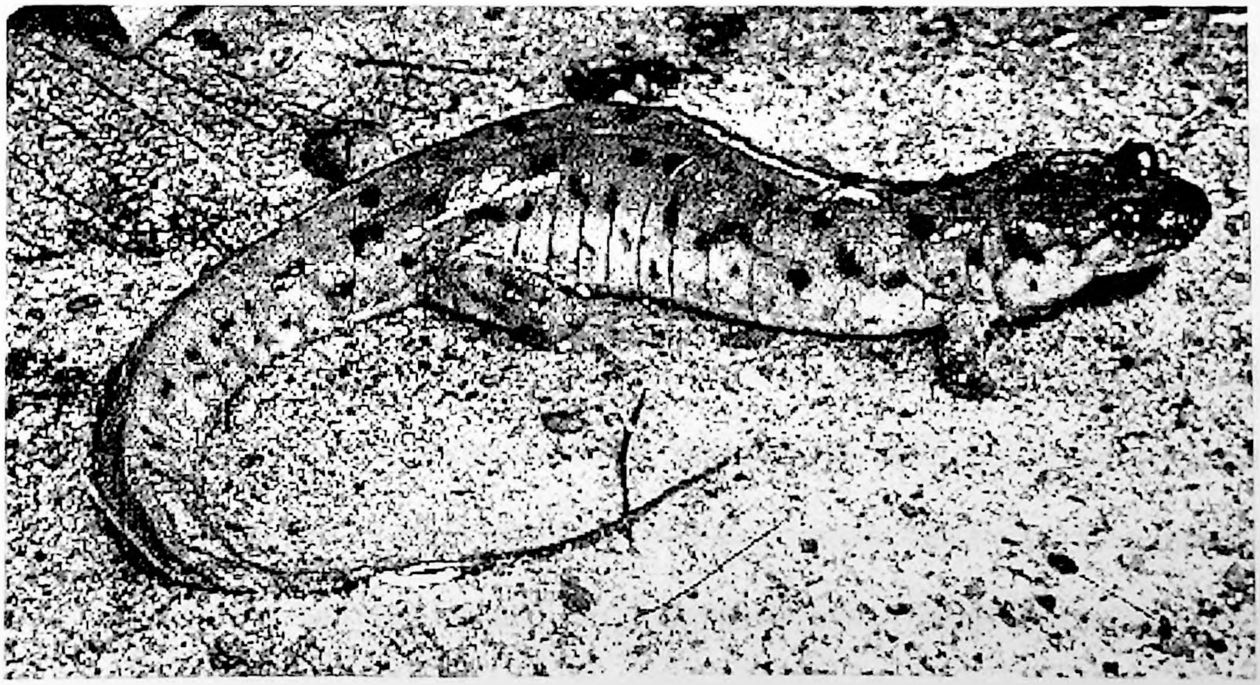
During the day, *D. fuscus* borrow in soft soil and stream banks and are found under leaves, rocks and logs. These salamanders are nocturnal and are easily found on top of rocks on warm, damp nights. Mating occurs in the spring and fall. Females lay eggs under logs and rocks near small woodland streams in mid-summer. The larval period is usually one year. The total range of *D. fuscus* extends from New Brunswick to South Carolina and is statewide in West Virginia (Green and Pauley, 1987; Conant and Collins, 1998).

Desmognathus monticola Dunn (seal salamander) is a dark brown, robust salamander with dark, wormlike markings on its back (Fig. 4). It is the largest *Desmognathus* species discussed in this thesis, attaining a total length of 14.0 cm. The tail is strongly keeled, and there are 14 costal grooves (Green and Pauley, 1987).

The seal salamander is found in cool mountain streams and is the most aquatic species listed here. It burrows in stream banks and can be found under rocks and moss in streams. These salamanders are extremely active at night, crawling and perching on the surface of rocks and along stream banks. Mating occurs in spring and eggs are laid from June through September in nests found in the stream bank (Marcum, 1994).

Figure 3. *Desmognathus fuscus* (Photo by R. Birch)

Figure 4. *Desmognathus monticola* (Photo by J.R. MacGregor)



Desmognathus monticola is found statewide in West Virginia and ranges from Pennsylvania to Alabama (Green and Pauley, 1987; Conant and Collins, 1998).

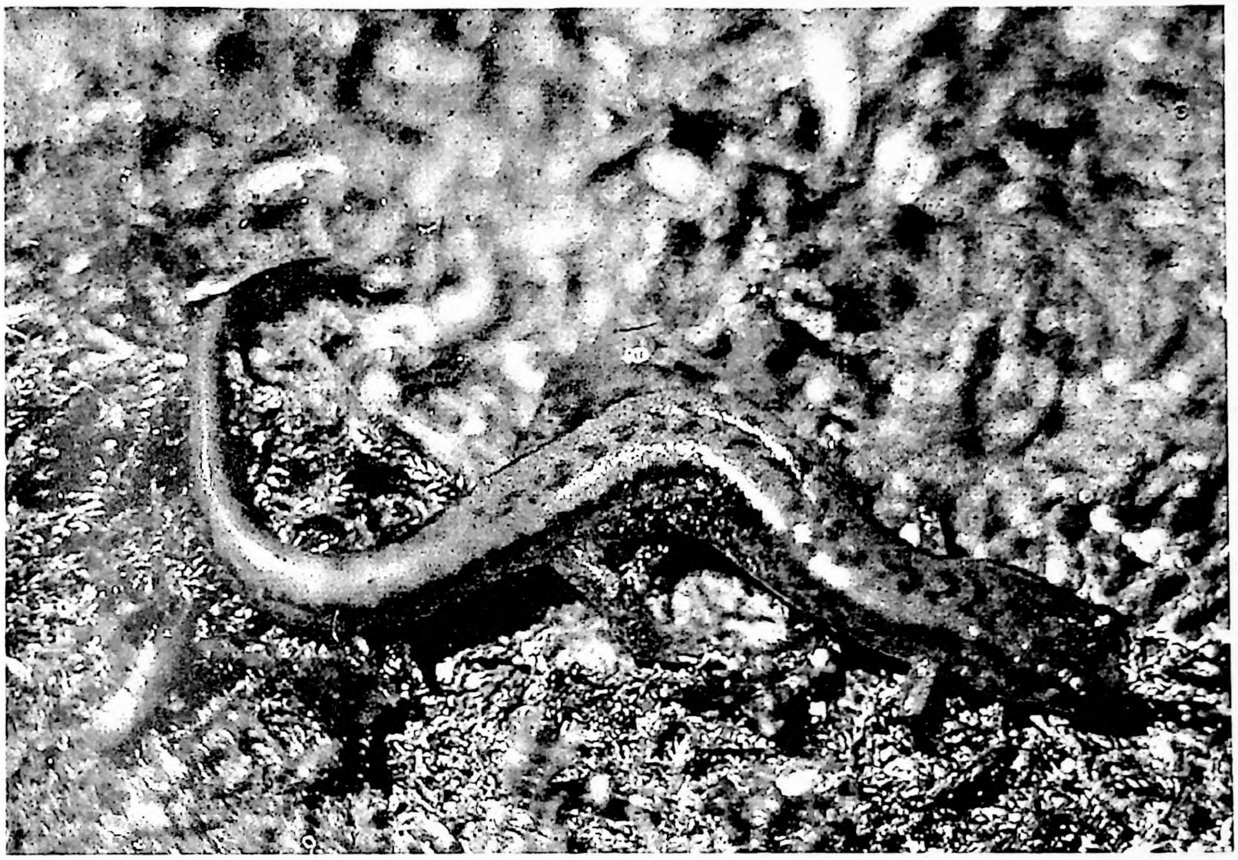
Desmognathus ochrophaeus Cope (mountain dusky) is a small salamander typically with a light dorsal stripe with straight, dark borders on each side. There are usually chevron markings down the middle dorsal stripe (Fig. 5). These markings, however, are extremely variable and this species is often confused with *D. fuscus*, *Plethodon cinereus* and *Eurycea bislineata*. This species reaches a total length of 10.2 cm and possesses a round tail (Green and Pauley, 1987).

Desmognathus ochrophaeus is the most terrestrial species of the genus in West Virginia. It is in streams, co-existing with *D. monticola* and *D. fuscus*, as well as on ridges and terrestrial habitats. The mountain dusky is found under leaf litter and rocks and has been found under the same coverboards as *P. cinereus* (pers. obs.). This species is active at night in both stream and terrestrial habitats. As other species in the genus, *D. ochrophaeus* mates in the spring and the female stays on a nest constructed beneath rocks, logs or in stream banks (Marcum, 1994). The mountain dusky is found in the mountainous counties in West Virginia and is found from New York to Alabama (Green and Pauley, 1987; Conant and Collins, 1998).

Plethodon cinereus (Green) (red-backed salamander) is a small terrestrial salamander with a straight-edged red stripe down the back (Fig. 6). The lead-back phase of this species has no dorsal stripe; however, the black and white speckled ventor is characteristic of all *P. cinereus*. This salamander reaches a total length of 10.2 cm and has a rounded tail and 18-19 costal grooves (Green and Pauley, 1987).

Figure 5. *Desmognathus ochrophaeus* (Photo by T.K. Pauley)

Figure 6. *Plethodon cinereus* (Photo by T.K. Pauley)



The red-back salamander is found under rocks, bark, logs and leaf litter during the day and forages for food at night. Mating occurs in the fall and spring and females stay on a nest constructed under logs or in crevices. *Plethodon cinereus* is probably distributed statewide in West Virginia except in western counties and ranges from Quebec to North Carolina (Green and Pauley, 1987).

Plethodon glutinosus (Green) (slimy salamander) is a large, black terrestrial salamander sprinkled with white spots (Fig. 7). This species can reach a total length of 20.3 cm and has 16 costal grooves. These salamanders produce a sticky, slimy secretion when handled. It is found in woodlands under cover objects and is active at night. Mating occurs in the spring and eggs hatch in late-summer. This species is distributed throughout West Virginia and ranges from New York to Florida (Green and Pauley, 1987)

Plethodon hoffmani Highton (ridge and valley salamander) is a dark slender salamander, often with light colored flecks on the dorsum (Fig. 8). The ridge and valley salamander reaches a total length of 12.7 cm and has 20-21 costal grooves. This terrestrial salamander is commonly found under rocks and logs in the spring and fall, but is not encountered as frequently in the summer. In West Virginia, *P. hoffmani* is only found in the eastern counties which constitute the Ridge and Valley province. Its total range is from Pennsylvania to Virginia (Green and Pauley, 1987).

All of these species are said to feed and be active at night. The habits of *D. ochrophaeus* are described as "seldom encountered in the daytime unless its place of concealment is uncovered" (Green and Pauley, 1987). During the year I conducted field work for this project, I frequently saw *D. ochrophaeus* walking through streams and on

Figure 7. *Plethodon glutinosus* (Photographer unknown)

Figure 8. *Plethodon hoffmani*

Photo not shown

the forest floor during daytime. This occurrence was so common on Plot 12, that I encountered one in this manner almost every month. The literature also stated that *P. cinereus* and *P. glutinosus* remain concealed during the day and forage for food at night (Green and Pauley, 1987). In the course of this field work, I encountered three *P. cinereus*, one large *P. glutinosus* and an ant nest under one common board site. All of these salamanders were actively feeding on ants under the coverboard during the day. These personal observations do not agree with the salamander literature and, thus, demonstrate the diversity of natural history strategies within a species. However, most of my observations were in agreement with the literature.

Results

Prey items in 687 salamanders were identified and measured. In 1995, 124 salamanders were taken from pitfall samples and 1996 and 1997, 71 and 145 salamanders, respectively. In 1997, 182 salamanders were hand-collected and 165 were collected in 1998.

Intraspecific comparisons: treatments

Twelve comparisons were made between treatments and six were made between pre- and post-treatment years for *D. ochrophaeus* and *P. cinereus*. I required a significant correlation for either prey taxa or prey size to consider a comparison (*Bt* vs Gypchek, Gypchek vs no treatment, *Bt* vs no treatment) significant. For example, *P. cinereus* did not have significant prey taxa overlap between *Bt* and Gypchek plots, but there was a significant overlap of prey size for this same comparison. Therefore, *P. cinereus* from *Bt* plots and Gypchek plots had significant dietary overlaps. Spearman rank correlation and Fisher's exact test (2-tail) had similar results for the comparisons discussed below except when otherwise noted.

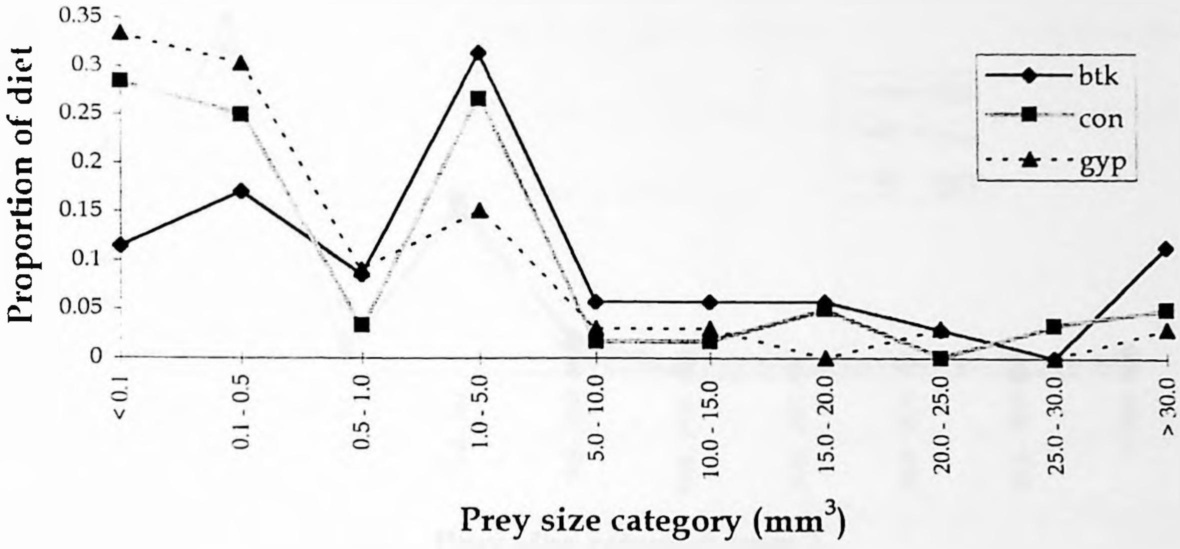
Significant dietary overlaps between treatments for *D. ochrophaeus* and *P. cinereus* for hand-collected samples are listed in table 4. Based on a positive correlation of either prey taxa or prey size analysis, the diets of hand-collected *P. cinereus* and *D. ochrophaeus* did not differ significantly between treatments (Spearman rank correlation, $p < 0.05$, Fisher's exact test, $p=0.231$). Trends of prey taxa and prey size between treatments for *D. ochropaeus* and *P. cinereus* are found in Figure 9a&b.

There were no significant overlaps of any pitfall specimen between treatments using Spearman rank correlation. However, Fisher's exact test (2-tail) did not show any

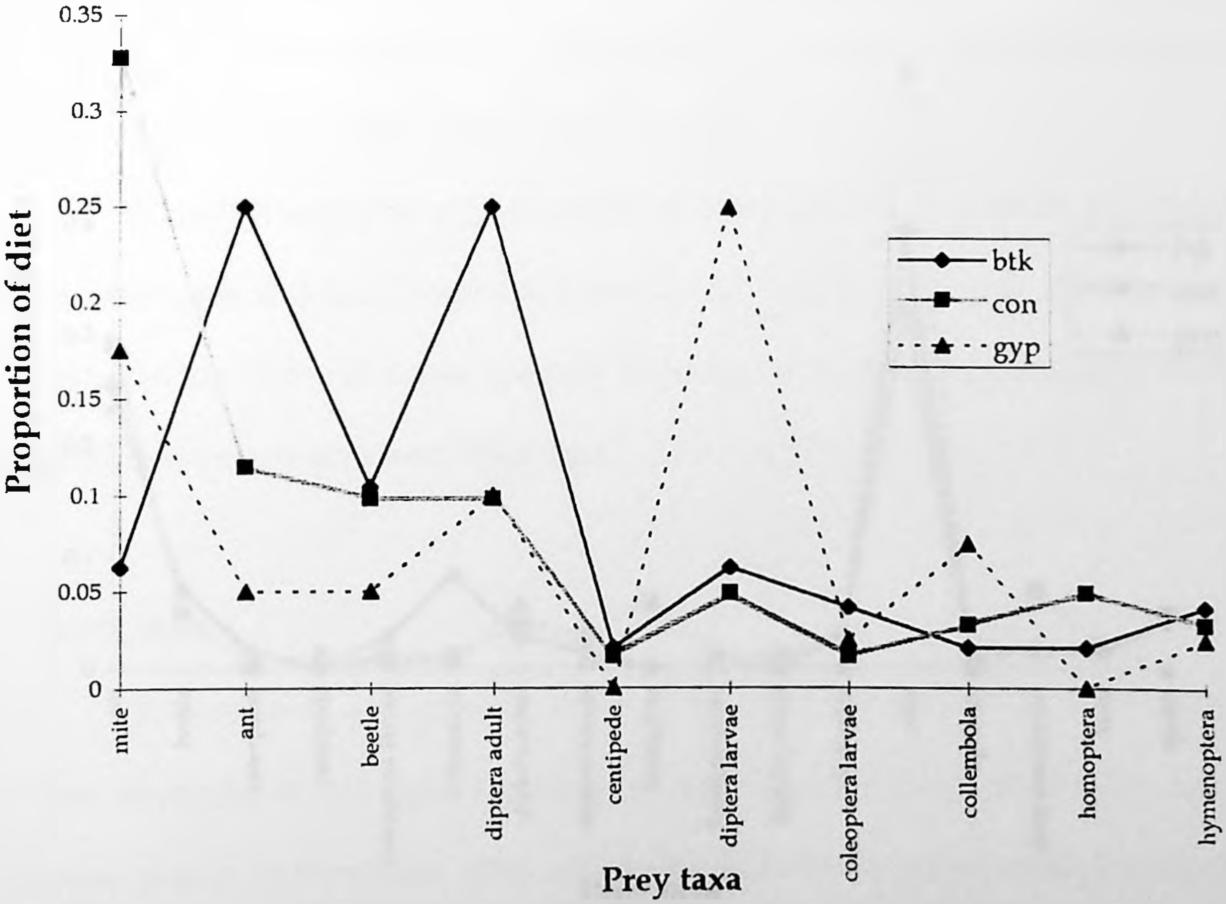
Table 4. Intraspecific comparisons between treatments for hand-collected *D. ochrophaeus* and *P. cinereus*. Asterisks mark comparisons significantly correlated (Spearman rank correlation, P=0.05; Fisher's exact test, P=0.231). For *D. ochrophaeus*, N_{Bt} =31, N_{none} =34 and N_{Gyp} =15. For *P. cinereus*, N_{Bt} =17, N_{none} =24 and N_{Gyp} =20.

Species	Treatment 1	Treatment 2	Prey Analysis	Significant Correlation
D. ochrophaeus	*Bt*	no treatment	taxa	*
	Bt	no treatment	size	*
	Gyp	no treatment	taxa	*
	Gyp	no treatment	size	*
	Bt	Gyp	taxa	*
	Bt	Gyp	size	*
P. cinereus	*Bt*	no treatment	taxa	
	Bt	no treatment	size	*
	Gyp	no treatment	taxa	
	Gyp	no treatment	size	*
	Bt	Gyp	taxa	
	Bt	Gyp	size	*

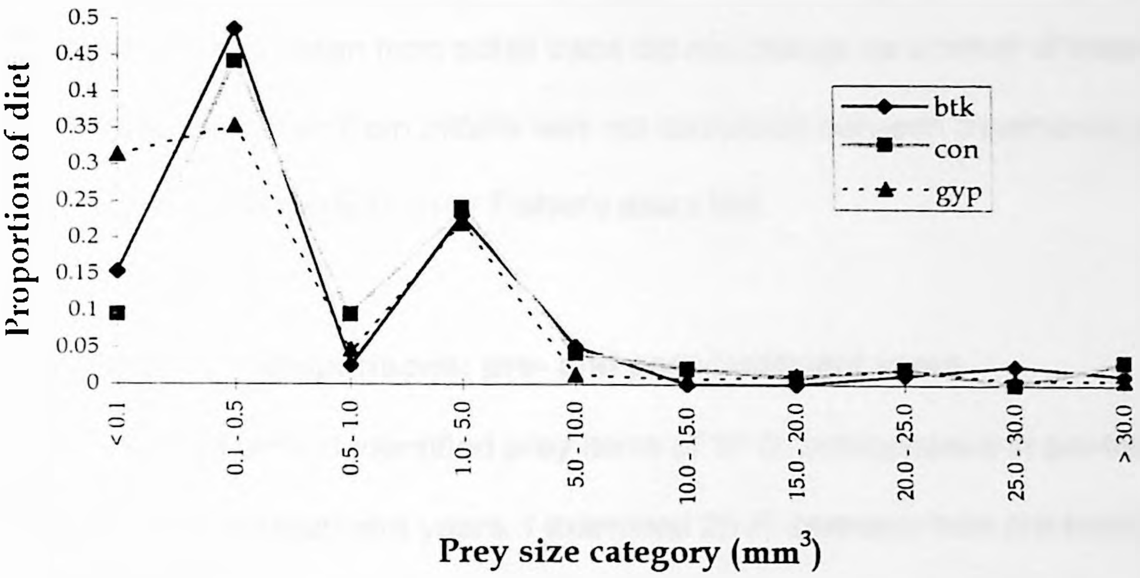
Figure 9a-d. Proportion of prey sizes and prey taxa in the diet of hand-collected *D.* ochrophaeus and P. *cinereus* from three treatments



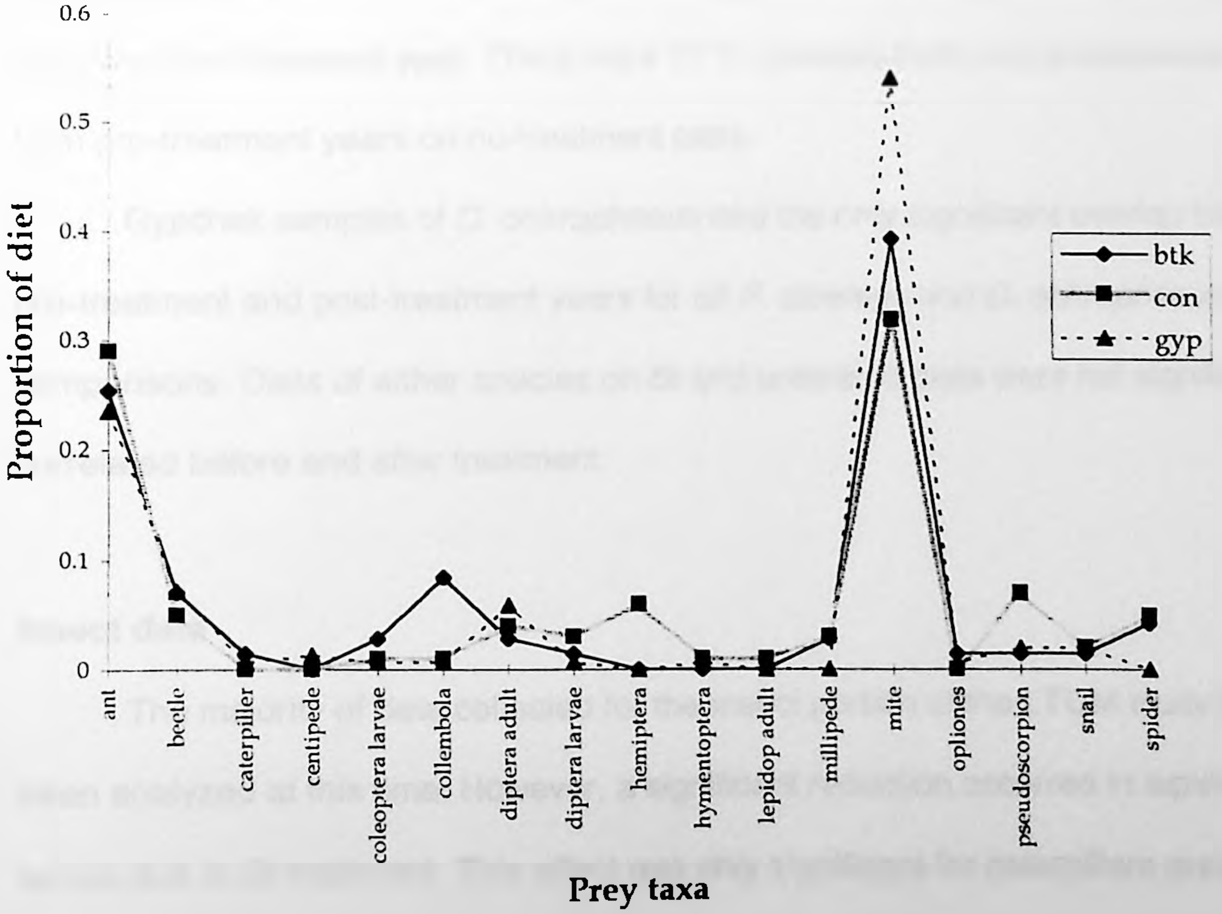
9a. Proportion of prey sizes in the diet of hand-collected *D. ochrophaeus* samples from three treatments



9b. Proportion of prey taxa in the diet of hand-collected *D. ochrophaeus* samples from three treatments



9c. Proportion of prey sizes in the diet of hand-collected *P. cinereus* from three treatments



9d. Proportion of prey taxa in diet of hand-collected *P. cinereus* from three treatments significant differences in the proportion of prey taxa of *D. ochrophaeus* between treatments (p=0.110) (Table 5). Based on Fisher's exact test, I assume that the diets of *D. ochrophaeus* taken from pitfall traps did not change as a result of treatment. The diet of *P. cinereus* taken from pitfalls was not correlated between treatments using either Spearman rank correlation or Fisher's exact test.

Intraspecific comparisons: pre- and post-treatment years

For *Bt* plots, I identified prey items of 37 *D. ochrophaeus* in pre-treatment years and 24 in post-treatment years. I examined 20 *P. cinereus* from pre-treatment *Bt* plots and 7 from post-treatment plots. Gypchek plots had 28 *D. ochrophaeus* before treatment and 27 after and 19 *P. cinereus* before treatment and 8 after treatment. Plots without pesticide application had 22 *D. ochrophaeus* from pre-treatment years and 9 from the post-treatment year. There were 17 *P. cinereus* from post-treatment and 18 from pre-treatment years on no-treatment plots.

Gypchek samples of *D. ochrophaeus* had the only significant overlap between pre-treatment and post-treatment years for all *P. cinereus* and *D. ochrophaeus* comparisons. Diets of either species on *Bt* and untreated plots were not significantly correlated before and after treatment.

Insect data

The majority of data collected for the insect portion of the LTGM study has not been analyzed at this time. However, a significant reduction occurred in lepidopteran larvae due to *Bt* treatment. This effect was only significant for caterpillars present at the

Table 5. Intraspecific comparisons between treatments for pitfall *D. ochrophaeus* and *P. cinereus*. Asterisk's mark comparison which do not differ significantly (Fisher's exact test, P=0.111). For *D. ochrophaeus*, N_{Bt} =24, N_{none} =22 and N_{Gyp} =27. For *P. cinereus*, N_{Bt} =7, N_{none} =17 and N_{Gyp} =8.

Species	Treatment 1	Treatment 2	Prey Analysis	Significant Difference
D. ochrophaeus	*Bt*	no treatment	taxa	*
	Bt	no treatment	size	
	Gyp	no treatment	taxa	*
	Gyp	no treatment	size	
	Bt	Gyp	taxa	*
	Bt	Gyp	size	
P. cinereus	*Bt*	no treatment	taxa	
	Bt	no treatment	size	
	Gyp	no treatment	taxa	
	Gyp	no treatment	size	
	Bt	Gyp	taxa	
	Bt	Gyp	size	

time of treatment and for 3 weeks thereafter. Larvae which hatched after that period were not significantly affected (Butler, pers. com.). Ant species richness, diversity, abundance and species composition did not change as a result of the treatments.

Interspecific comparisons: food overlap

Table 6 lists the proportion of prey taxa in the diets of the six salamander species compared for feeding niche overlaps. All species consumed a wide variety of prey items. Only items present in 10 or more percent of the diet were used in statistical analyses. Prey taxa overlaps were found between 5 of 15 species pairs (Table 7).

Adult dipterans were the most abundant insects in the diets of semi-aquatic salamanders and formicids and Acari were most abundant in the diets of terrestrial species. Coleopterans composed approximately 10 percent of the diets of all salamanders. Figures 10a-f show The percentages of these prey items in the diets of each salamander species are found in Figure 10a-f. The percentage of adult dipterans, formicids and Acari varies between aquatic and terrestrial species (Fig. 10).

Based on dehydration tolerances and frequency of salamanders found in different habitats (Pauley and Raimondo, unpub. data), salamanders were plotted on a continuum from most terrestrial to most aquatic (Figs. 11-12). Formicids were found to significantly decrease in species which tend toward the aquatic end of the continuum ($r=-0.92$, $p=0.01$)(Fig. 11). Similar results occur in the percentage of adult dipterans found in diets. The proportion increases in salamanders toward the aquatic extreme of the continuum ($r=0.93$, $p=0.008$)(Fig. 12).

Table 6. Proportions of prey items in the diets of each species for 1997 and 1998.

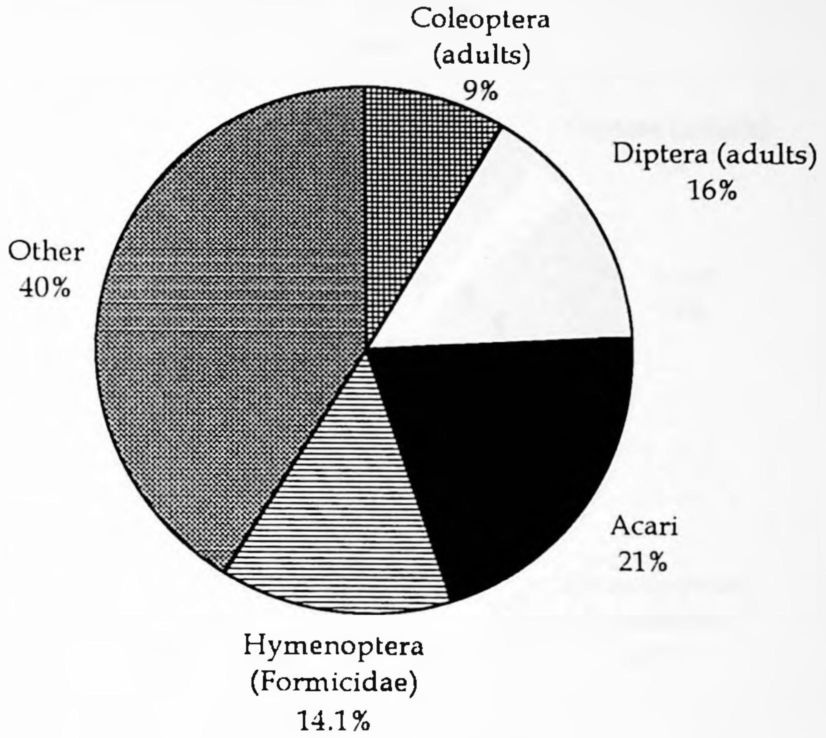
Prey item	Salamander Species					
	D. fuscus (N=53)	*D. monticola* (N=89)	*D. ochrophaeus* (N=98)	*P. cinereus* (N=61)	*P. glutinosus* (N=47)	*P. hoffmani* (N=27)
Acari	0.039	0.009	0.207	0.441	0.139	0.357
Araneae	0.132	0.035	0.067	0.031	0.046	0.009
Benthic invertebrates	0.039	0.086				
Chilopoda/Diplopoda	0.013	0.017	0.033	0.021	0.118	0.012
Coleoptera (adult)	0.171	0.087	0.087	0.065	0.107	0.04
Collembola	0.039	0.013	0.04	0.025	0.054	0.022
Decapoda		0.004				
Diptera (adult)	0.276	0.536	0.155	0.046	0.034	
Diptera (larvae)		0.03	0.107	0.015	0.004	0.016
Homoptera/Hemiptera	0.069	0.013	0.027	0.018	0.023	
Hymenoptera (Formicidae)	0.118	0.048	0.141	0.256	0.211	0.5
Hymenoptera (adult)			0.034	0.006		
Lepidoptera (adult)	0.039	0.048	0.013	0.003		
Lepidoptera (larvae)		0.013		0.006	0.038	
Mecoptera	0.013	0.009	0.007			
Miscellaneous larvae	0.013	0.013	0.027	0.012	0.076	0.012
Orthoptera			0.007		0.031	
Plecoptera	0.013	0.009				
Pseudoscorpion			0.007	0.034	0.031	0.028
Gastropoda	0.026	0.004	0.034	0.021	0.088	0.004
Salamander larvae		0.004				
Trichoptera		0.022	0.007			

Table 7. Spearman rank correlation of prey taxa found in the diets of 15 species pairs (P = 0.05).

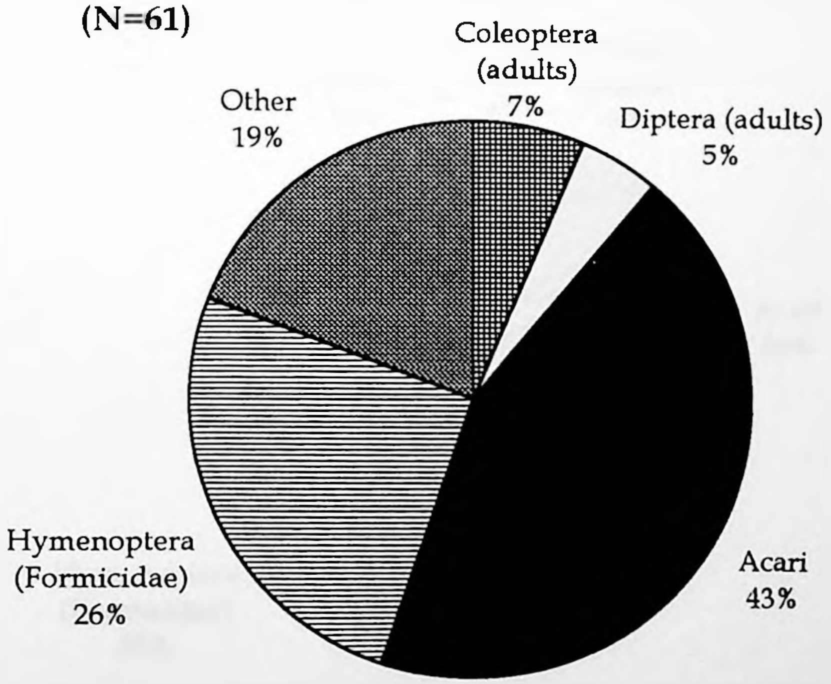
Species 1	Species 2	Correlation
D. fuscus	*D. monticola*	*
D. fuscus	*D. ochrophaeus*	
D. fuscus	*P. cinereus*	*
D. fuscus	*P. glutinosus*	
D. fuscus	*P. hoffmani*	
D. monticola	*D. ochrophaeus*	
D. monticola	*P. cinereus*	
D. monticola	*P. glutinosus*	
D. monticola	*P. hoffmani*	
D. ochrophaeus	*P. cinereus*	*
D. ochrophaeus	*P. glutinosus*	
D. ochrophaeus	*P. hoffmani*	
P. cinereus	*P. glutinosus*	*
P. cinereus	*P. hoffmani*	*
P. glutinosus	*P. hoffmani*	

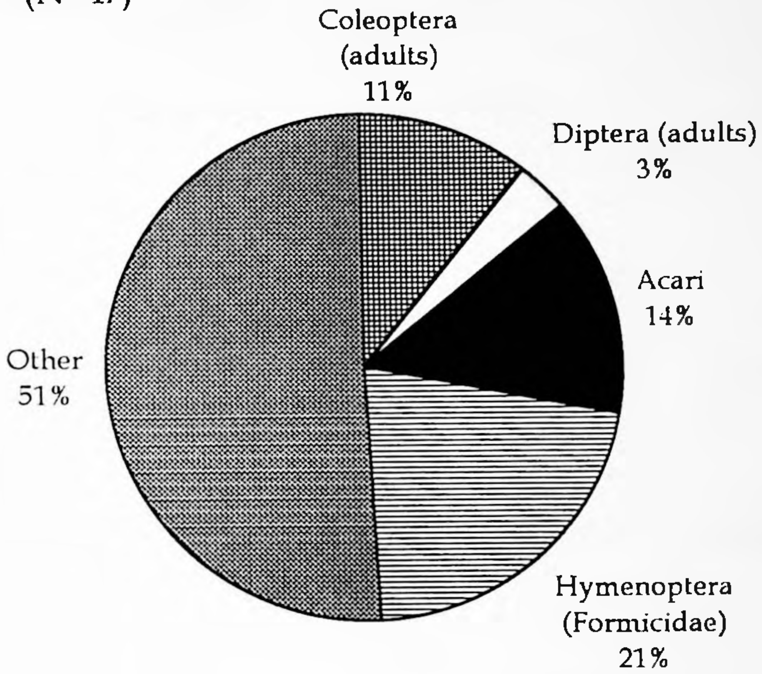
Figure 10a-f. Percent of primary food items in six species of salamanders

10c. Percent of Primary Food Items in *Desmognathus ochrophaeus* (N=98)



10d. Percent of Primary Food Items of *Plethodon cinereus* (N=61)




10e. Percent of Primary Food Items of *P. glutinosus* (N=47)

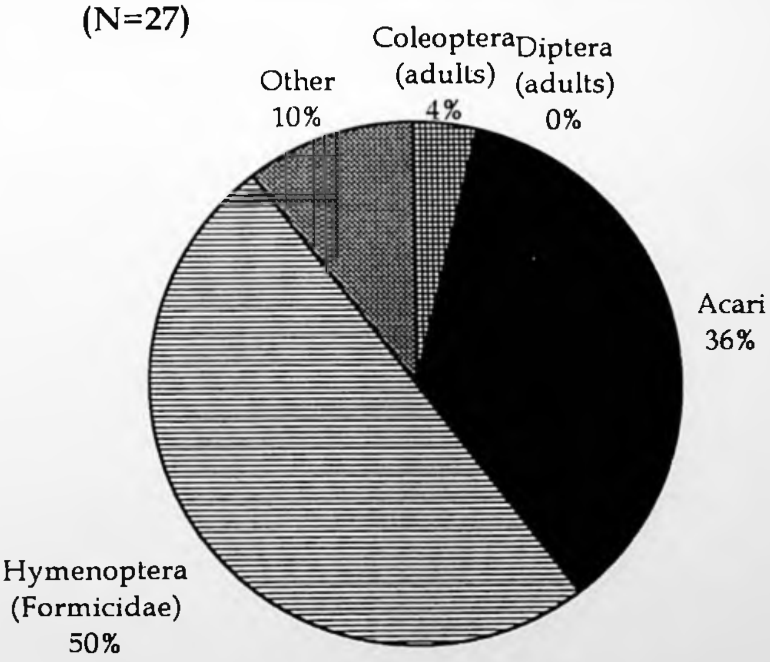

10f. Percent of Primary Food Items of *P. hoffmani* (N=27)

Figure 11. Percent formicids in salamanders diets

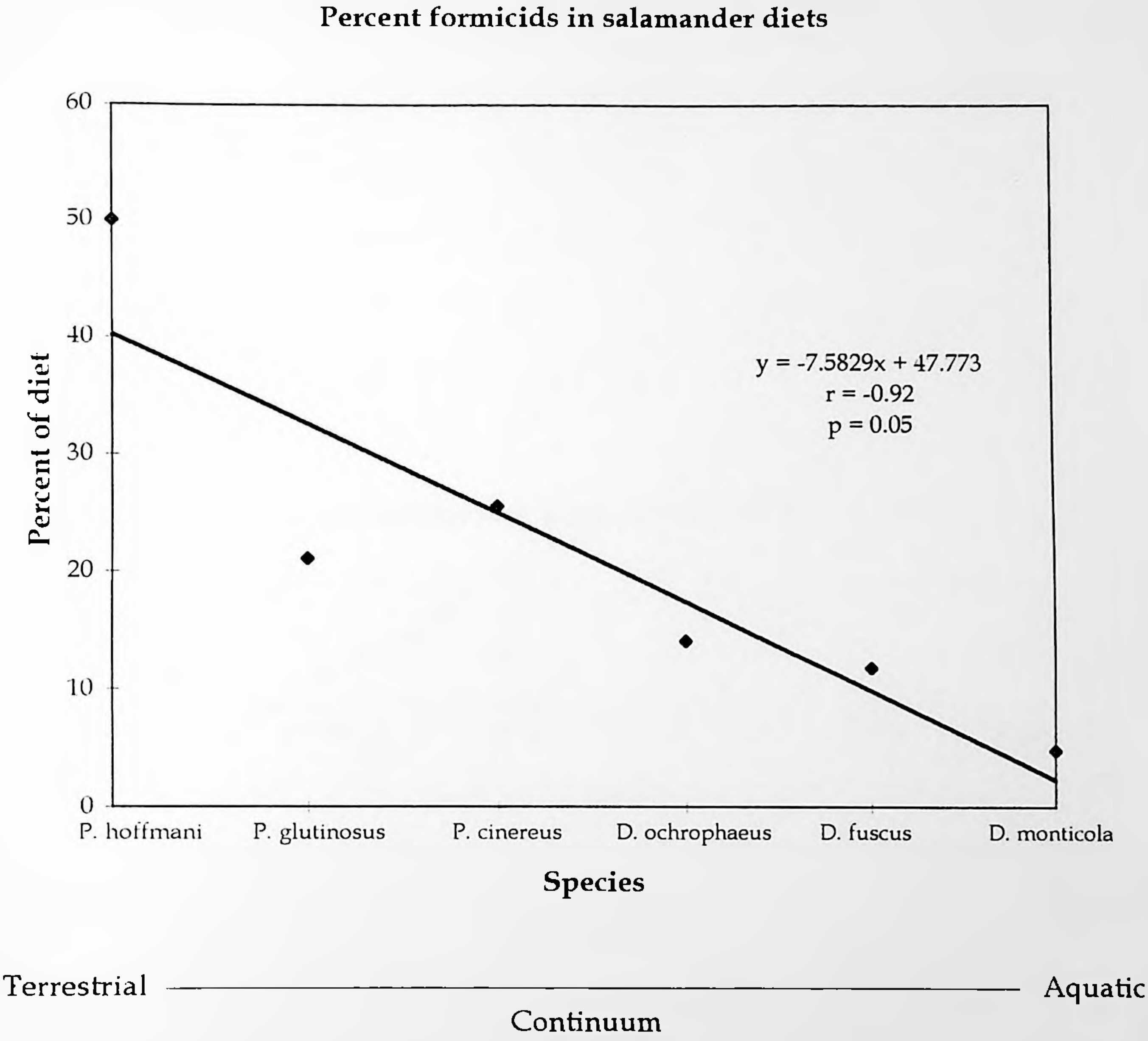
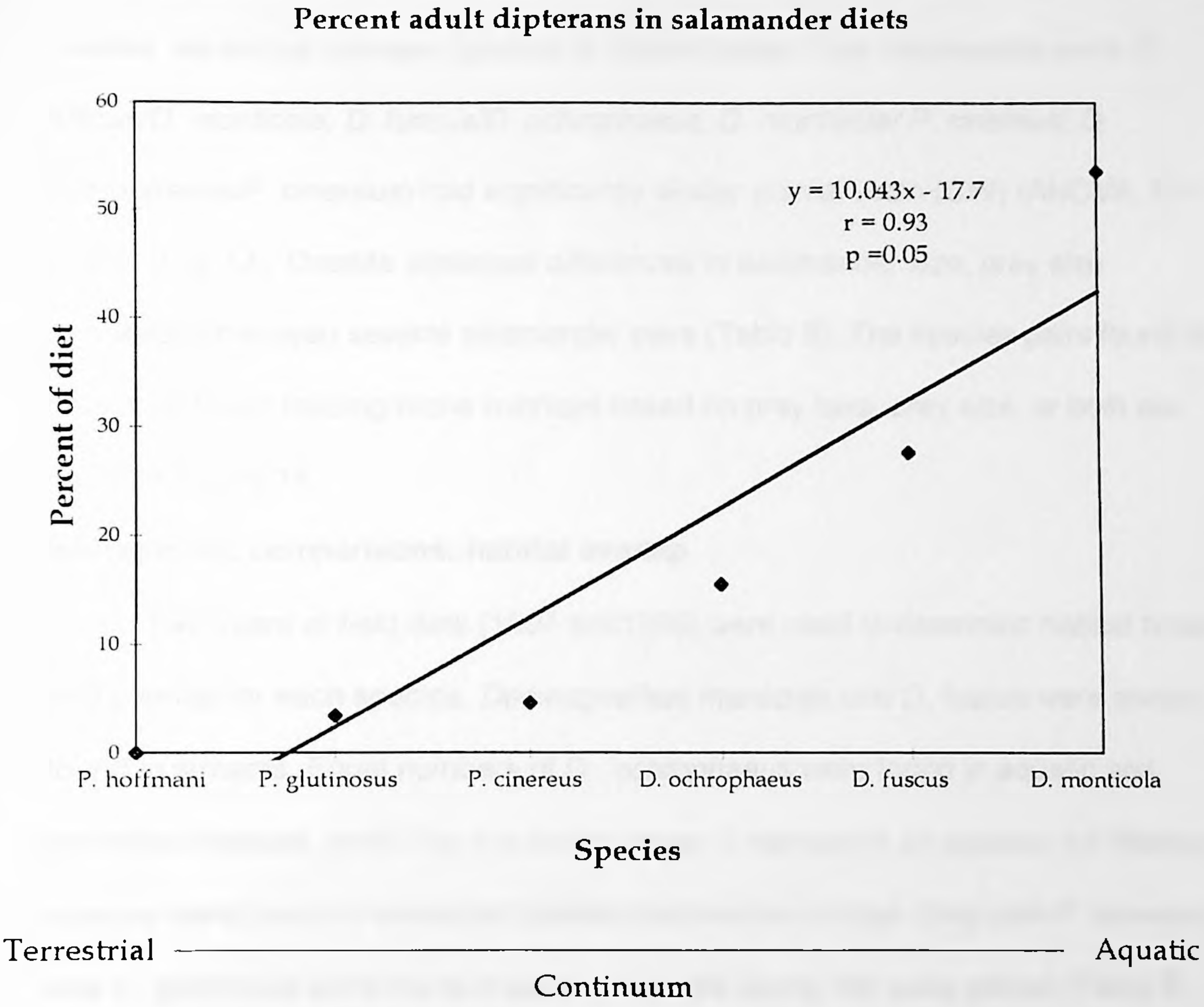

Percent formicids in salamander diets
Percent of diet
60
50
40
30
20
10
0
y = -7.5829x + 47.773
r = -0.92
p = 0.05
P. hoffmani
P. glutinosus
P. cinereus
D. ochrophaeus
D. fuscus
D. monticola
Species
Terrestrial
Aquatic
Continuum

Figure 12. Percent adult dipterans in salamander diets


Percent adult dipterans in salamander diets
y = 10.043x - 17.7
r = 0.93
p =0.05
Percent of diet
0
10
20
30
40
50
60
P. hoffmani
P. glutinosus
P. cinereus
D. ochrophaeus
D. fuscus
D. monticola
Species
Terrestrial
Aquatic
Continuum

Overlaps in prey sizes occurred between salamander species of similar size classes, as well as between species of different sizes. Four salamander pairs (*D. fuscus/D. monticola, D. fuscus/D. ochrophaeus, D. monticola/ P. cinereus, D. ochrophaeus/P. cinereus*) had significantly similar cranial width (CW) (ANOVA, $P < 0.001$) (Fig. 13). Despite statistical differences in salamander size, prey size overlapped between several salamander pairs (Table 8). The species pairs found to have significant feeding-niche overlaps based on prey taxa, prey size, or both are found in Figure 14.

Interspecific comparisons: habitat overlap

Two years of field data (1997 and1998) were used to determine habitat breadth and overlap for each species. *Desmognathus monticola* and *D. fuscus* were always found in streams. Equal numbers of *D. ochrophaeus* were found in aquatic and terrestrial habitats, exhibiting the widest range of habitats of all species. All *Plethodon* species were found in terrestrial habitats from ravine to ridge. Only one *P. cinereus* and one *P. glutinosus* were found in aquatic habitats during the study period (Table 9).

Desmognathus ochrophaeus had the widest niche breadth (45%), ranging from aquatic habitats to at least 100m toward the ridge. All *Plethodon* species were found throughout the terrestrial transects and also exhibited wide niche breadths (*P. cinereus* 41%, *P. glutinosus* 31%, *P. hoffmani* 44%). Both *D. monticola* and *D. fuscus* were only found in aquatic habitats and had extremely low niche breadths (0%) (Fig. 15a-f).

Desmognathus fuscus and *D. monticola* had 100% niche overlaps. There were less than 1% niche overlaps of *Plethodon* species with either *D. fuscus* or *D. monticola*.

Figure 13. Average cranial width of salamanders

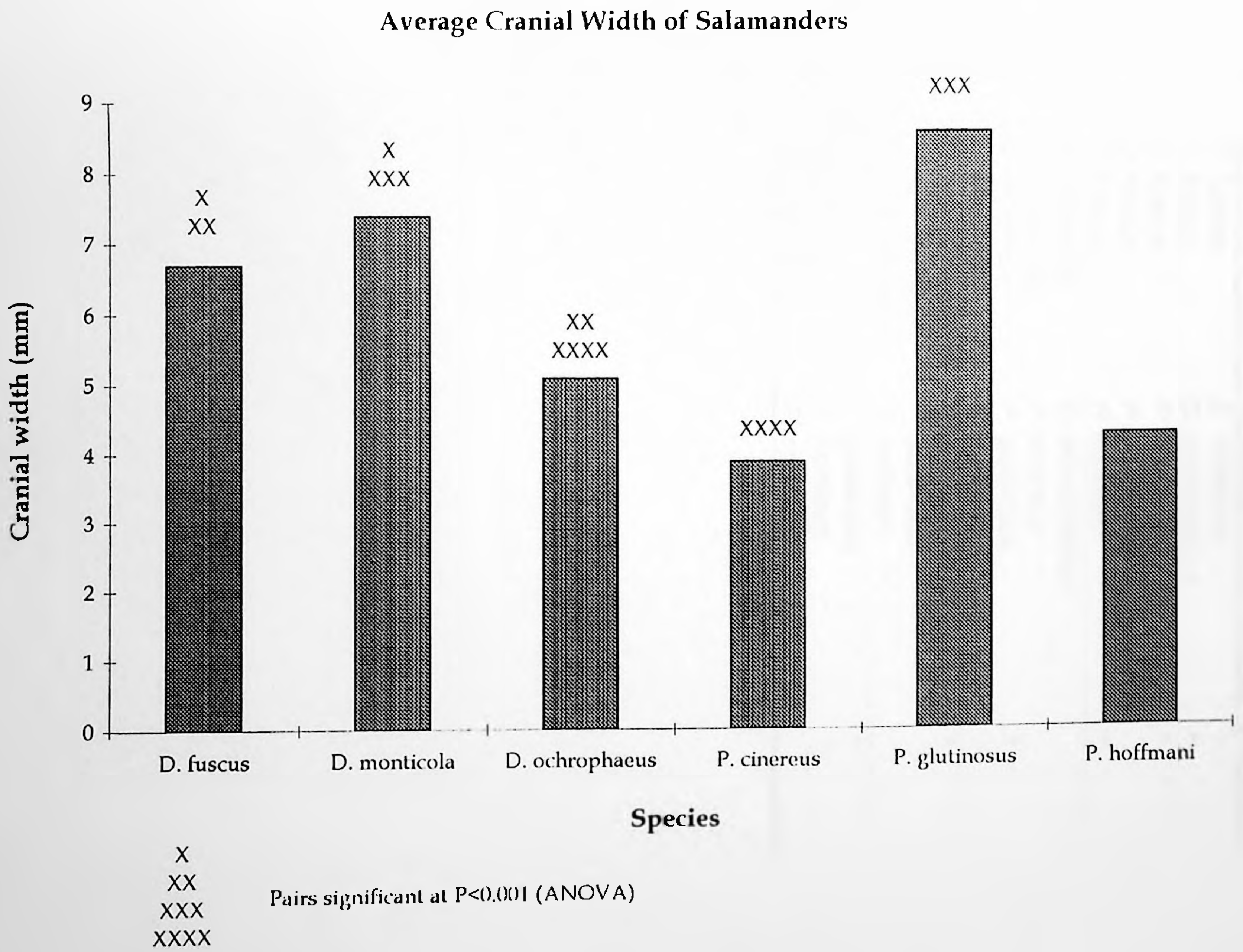

Average Cranial Width of Salamanders
Cranial width (mm)
9
8
7
6
5
4
3
2
1
0
X
XX
X
XXX
XX
XXXX
XXXX
XXX
D. fuscus
D. monticola
D. ochrophaeus
P. cinereus
P. glutinosus
P. hoffmani
Species
X
XX
XXX
XXXX
Pairs significant at P<0.001 (ANOVA)

Table 8. Spearman rank correlation of prey sizes found in the diets of 15 species pairs (P = 0.05).

Species 1	Species 2	Correlation
D. fuscus	*D. monticola*	
D. fuscus	*D. ochrophaeus*	*
D. fuscus	*P. cinereus*	*
D. fuscus	*P. glutinosus*	
D. fuscus	*P. hoffmani*	*
D. monticola	*D. ochrophaeus*	
D. monticola	*P. cinereus*	
D. monticola	*P. glutinosus*	*
D. monticola	*P. hoffmani*	
D. ochrophaeus	*P. cinereus*	*
D. ochrophaeus	*P. glutinosus*	
D. ochrophaeus	*P. hoffmani*	
P. cinereus	*P. glutinosus*	*
P. cinereus	*P. hoffmani*	*
P. glutinosus	*P. hoffmani*	

Figure 14. Feeding niche overlaps based on food (prey taxa and size). Thick bars represent significant overlaps and thin dashed bars are comparisons that were not significantly similar.

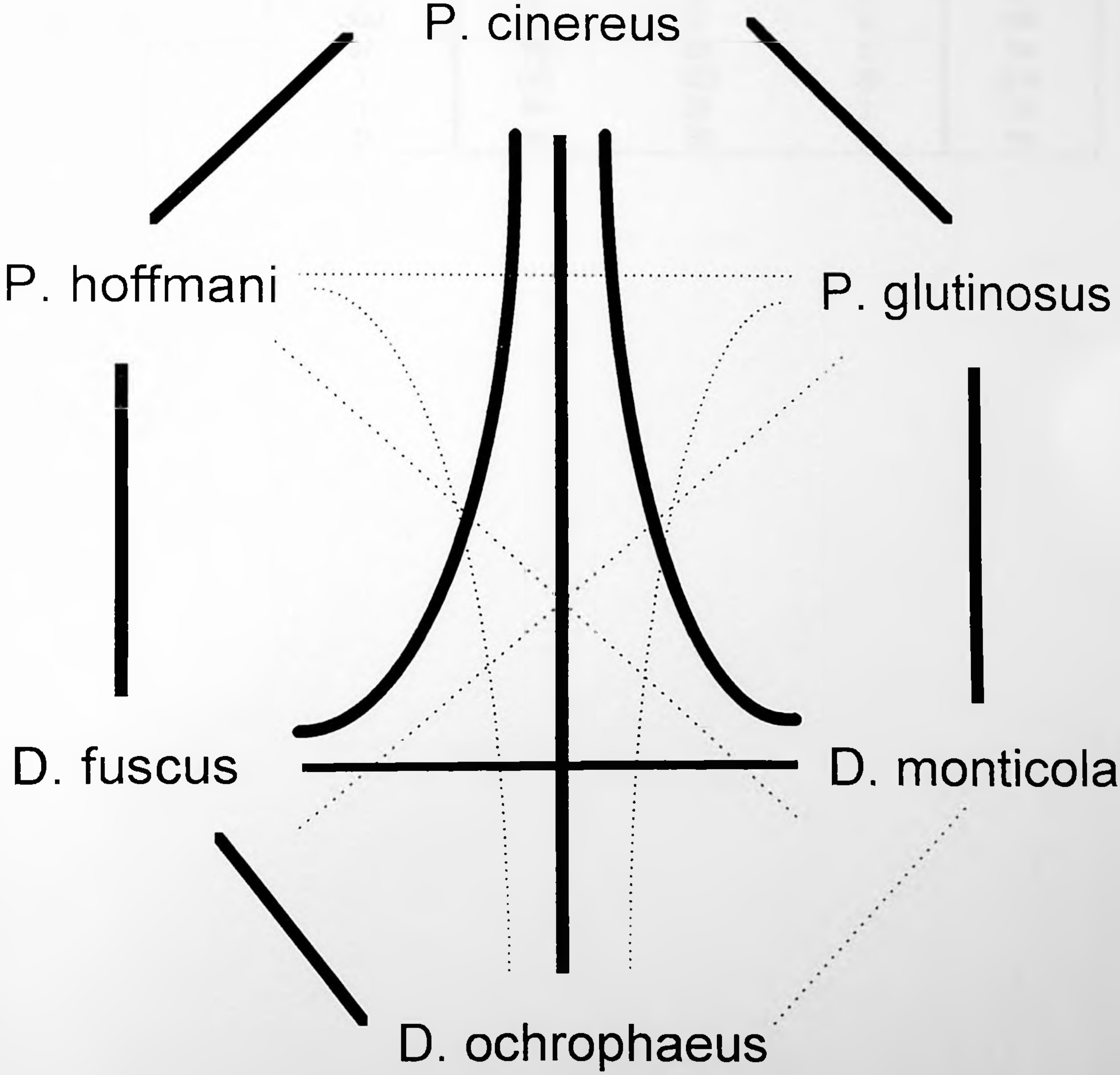
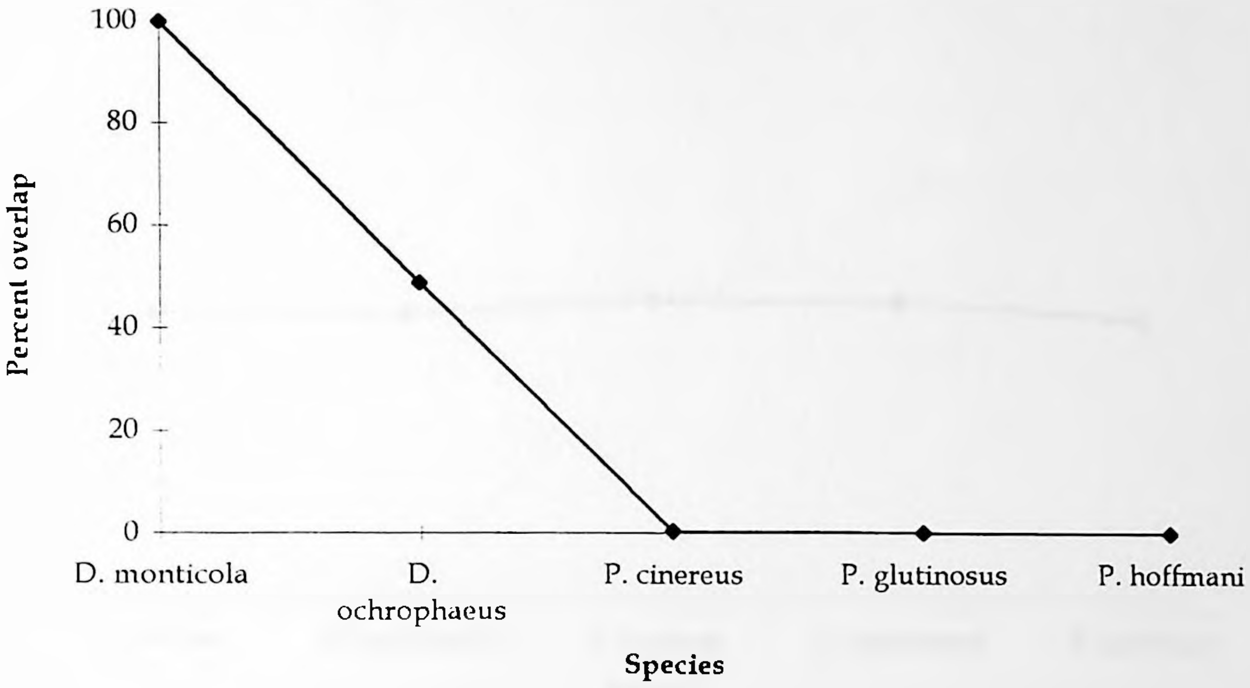

P. cinereus
P. hoffmani
P. glutinosus
D. fuscus
D. monticola
D. ochrophaeus

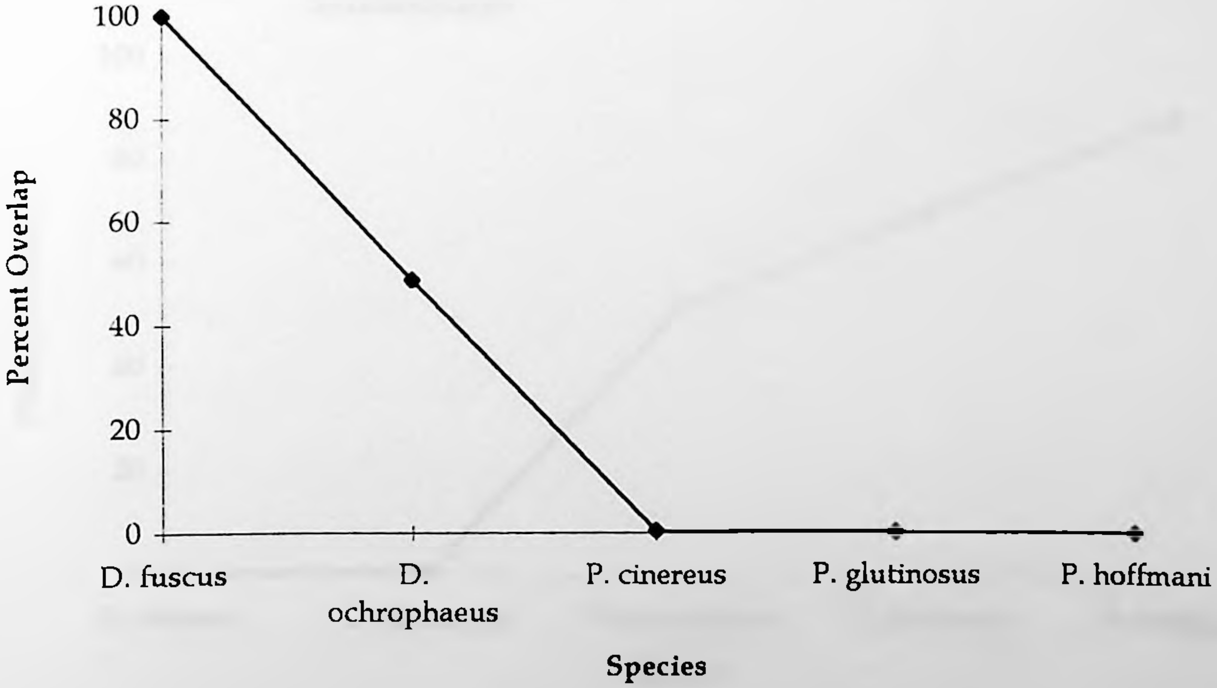
Table 9. Total number of salamanders found on aquatic and terrestrial transects. Terrestrial transects are divided into 3 niches based on elevation. Numbers are totals of 1997 and 1998 data.

Species	Aquatic (Stream)	Terrestrial 0-50 m	50-100m	Ridge	Total
D. fuscus	84	0	0	0	84
D. monticola	250	0	0	0	250
D. ochrophaeus	37	16	23	0	76
P. cinereus	1	110	123	22	256
P. glutinosus	1	56	21	1	79
P. hoffmani	0	44	35	15	94

Figure 15a-f. Habitat overlap of salamanders

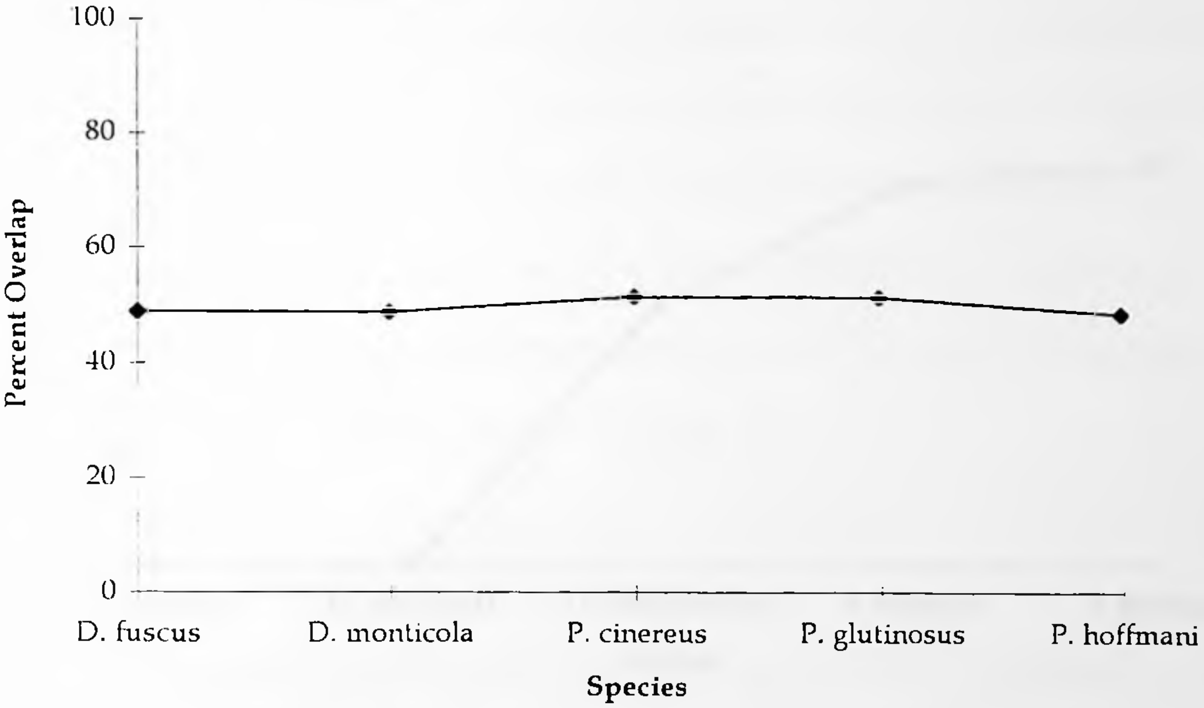


15a. Habitat Overlaps of D. *fuscus* with Five Other Species

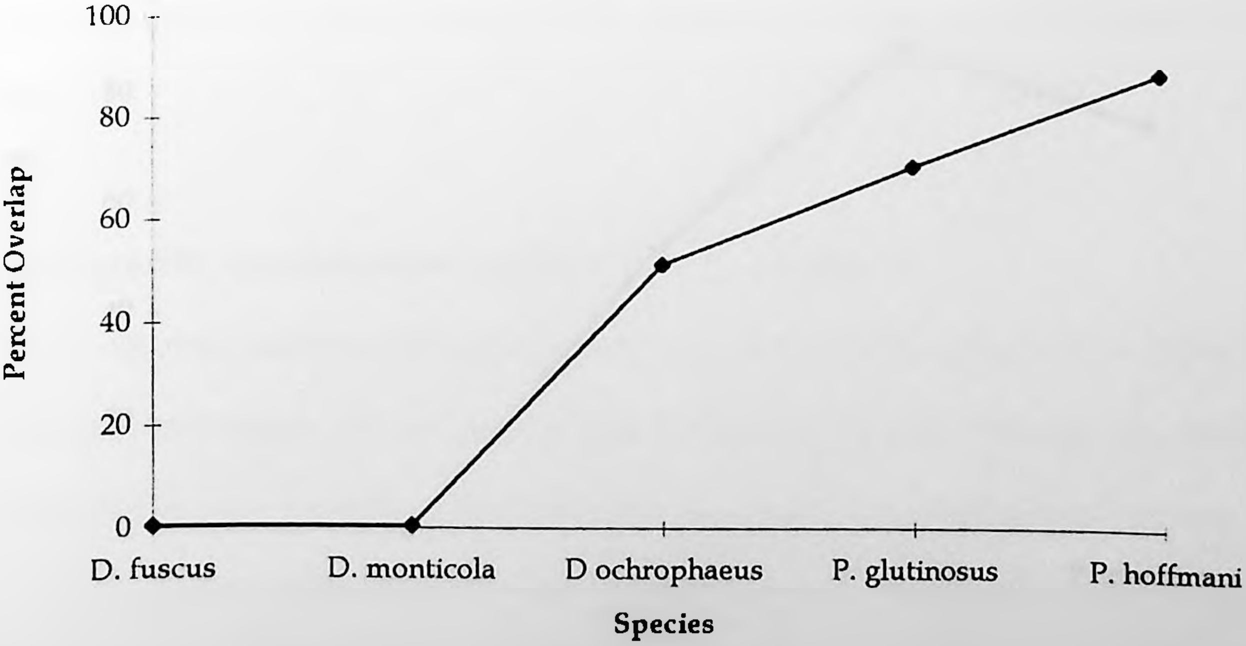


15b. Habitat Overlaps of D. *monticola* with Five Other Salamanders

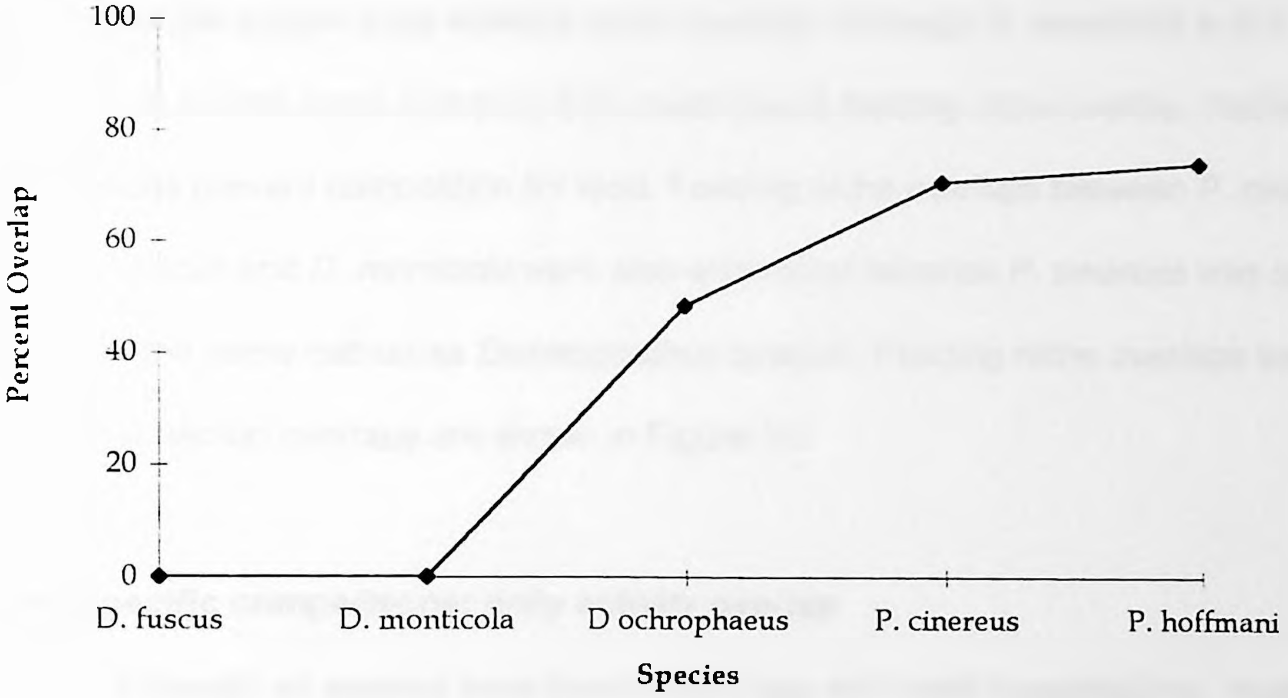
15c. Habitat Overlaps of *D. ochrophaeus* with Five Other Salamanders



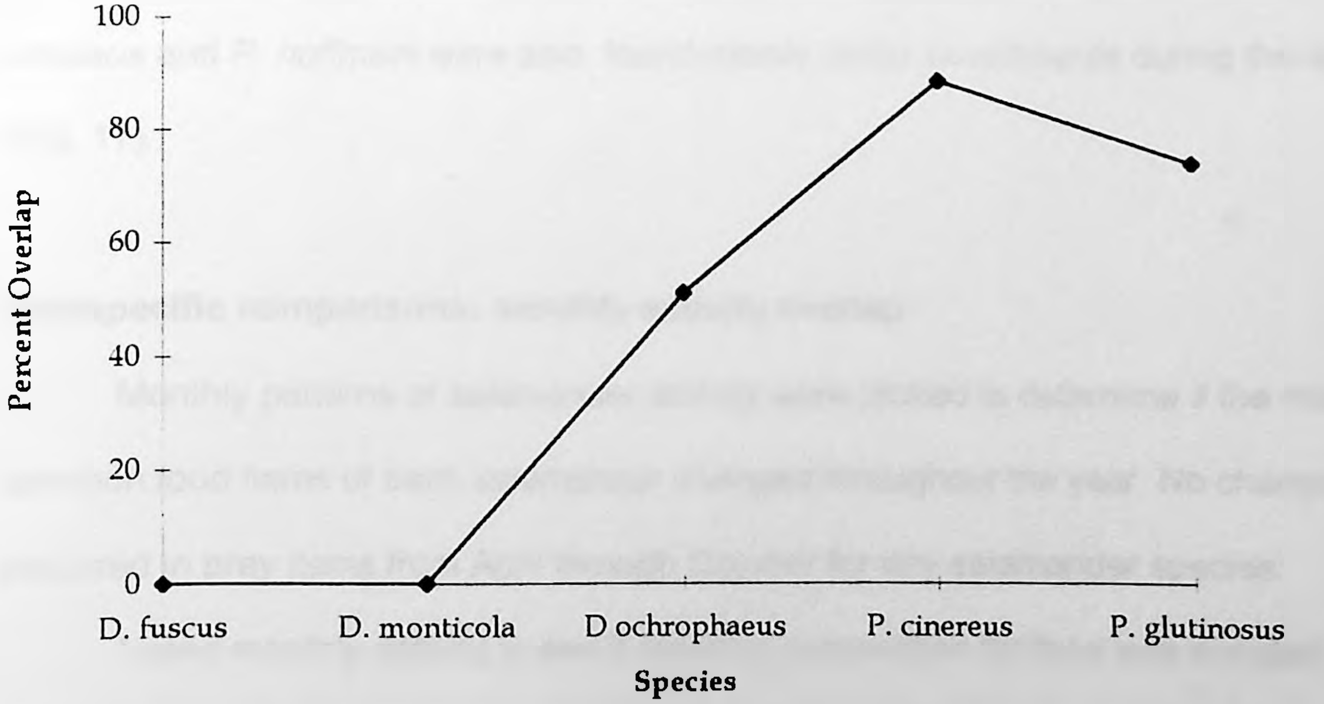
15d. Habitat Overlaps of *P. cinereus* with Five Other Salamanders



15e. Habitat Overlaps of *P. glutinosus* with Five Other Salamanders



15f. Habitat Overlap of *P. hoffmani* with Five Other Salamanders



Niche overlaps occurred to varying degrees between *D. ochrophaeus* and all species. *Plethodon* species had large niche overlaps within the genus.

Habitat further limits feeding niche overlaps. Although *D. monticola* and *P. glutinosus* ate the same size prey and could have a feeding niche overlap, habitat differences prevent competition for food. Feeding niche overlaps between *P. cinereus* and *D. fuscus* and *D. monticola* were also eliminated because *P. cinereus* was seldom found in the same habitat as *Desmognathus* species. Feeding niche overlaps based on food and habitat overlaps are shown in Figure 16.

Interspecific comparisons: daily activity overlap

Although all species were found during day and night investigations, most salamanders were found under cover objects during the day. Most *D. monticola* and *P. glutinosus* were found at night, 63 percent and 72 percent, respectively. Only 11 percent of *D. fuscus*, 30 percent of *D. ochrophaeus* were found at night. *Plethodon cinereus* and *P. hoffmani* were also found mostly under coverboards during the day (Fig. 17).

Interspecific comparisons: monthly activity overlap

Monthly patterns of salamander activity were plotted to determine if the most common food items of each salamander changed throughout the year. No changes occurred in prey items from April through October for any salamander species.

I used monthly activity to see if potential competition for food was avoided between species with food and habitat overlaps because species were active at

Figure16. Feeding niche overlaps based on food and habitat

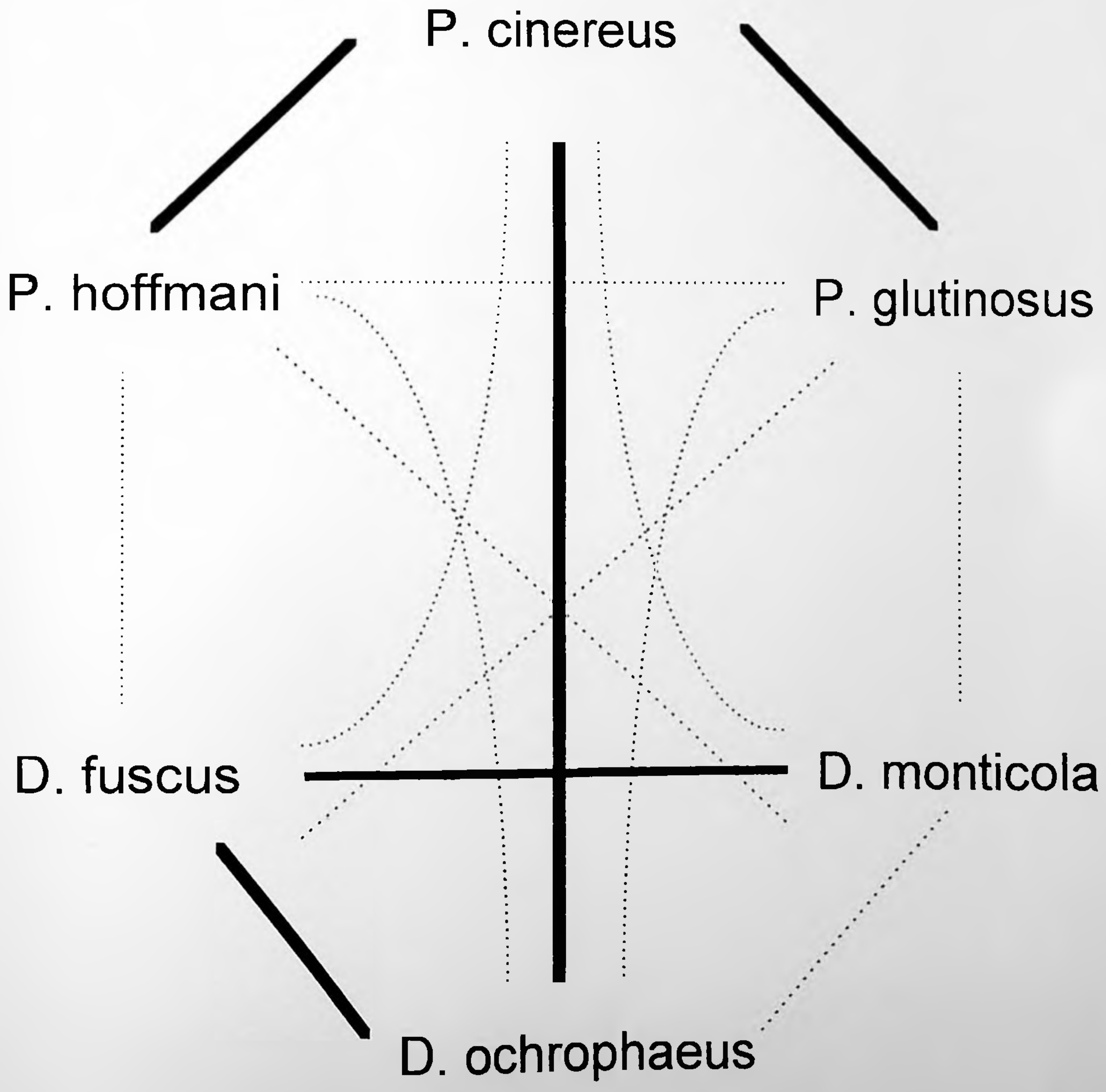
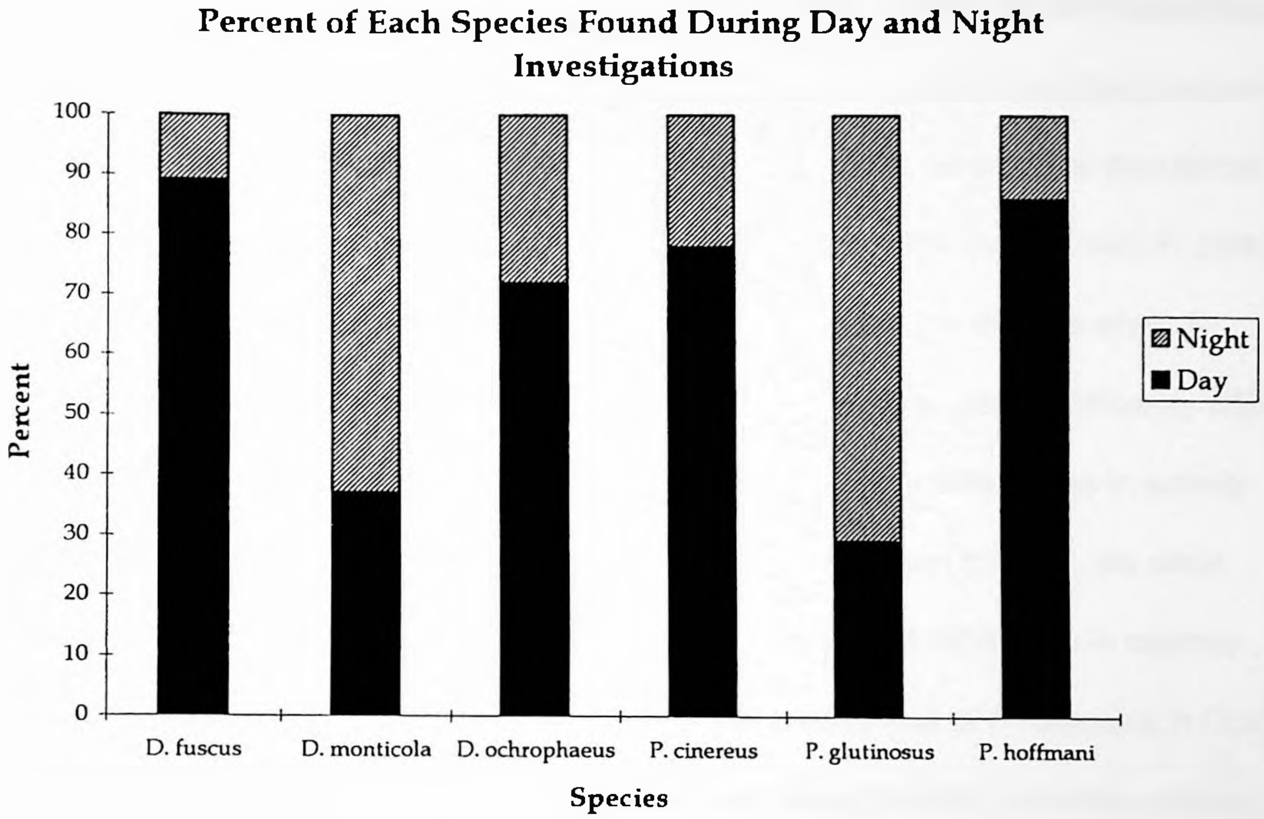

P. cinereus
P. hoffmani
P. glutinosus
D. fuscus
D. monticola
D. ochrophaeus

Figure 17. Percent of each species found during day and night investigations


Percent of Each Species Found During Day and Night Investigations
100
90
80
70
60
50
40
30
20
10
0
Percent
▨ Night
■ Day
D. fuscus
D. monticola
D. ochrophaeus
P. cinereus
P. glutinosus
P. hoffmani
Species

different times of the year. Monthly peaks of activity were plotted for each salamander species (Fig. 18). I found *P. hoffmani* was most active during April and May and was not found again until October. Conversely, all other species were active throughout the year. *Plethodon hoffmani*, which has a potential feeding niche overlap with *P. cinereus* based on prey taxa, prey size and habitat, was not found in the months when *P. cinereus* was most commonly found (Fig. 19). Monthly activity was significantly different for these two species (X^2=17.8, d.f=5,p=0.005). The monthly differences in activity between these two species could reduce potential competition for food. No other species pairs with food and habitat overlap had a significant difference in monthly activity. On the contrary, with the exception of the activity rise of *P. cinereus* in October, *P. cinereus* and *D. ochrophaeus* have remarkably similar trends in monthly activity (Fig. 20).

Predator-prey size relationship

Cranial width was used to determine if there was a relationship between predator size and prey volume, however, since CW was not measured in 1997, only 1998 data was used for this analysis. There was a significant correlation between salamander CW and prey volume (r=0.80, p=0.05) (Fig. 21), confirming larger salamanders eat larger prey items. The positive relationship between salamander CW and prey volume assumes that the species with significantly similar CW would eat similar size prey items.

Figure 18. Monthly activity of salamanders

Monthly Activity of All Salamanders

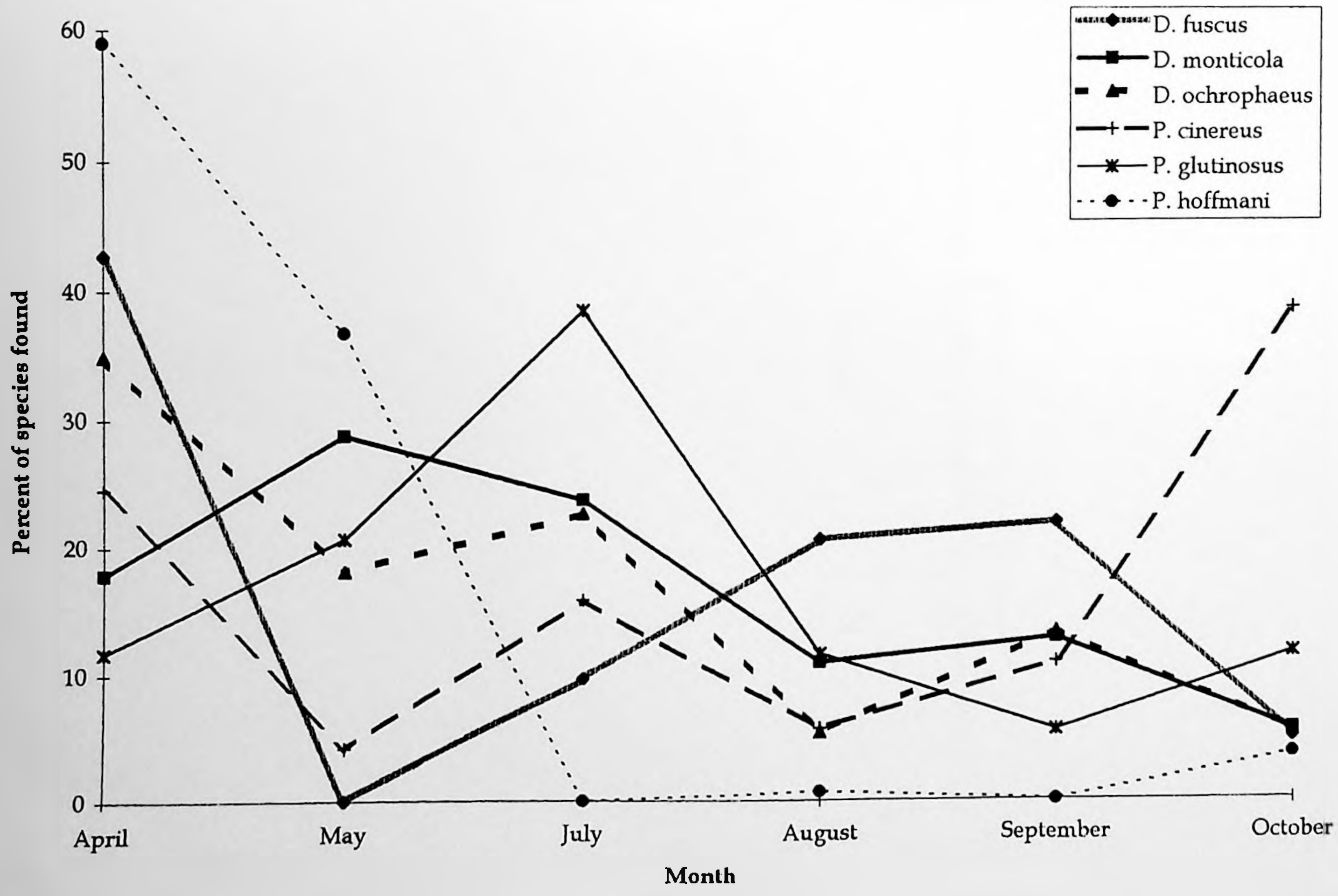
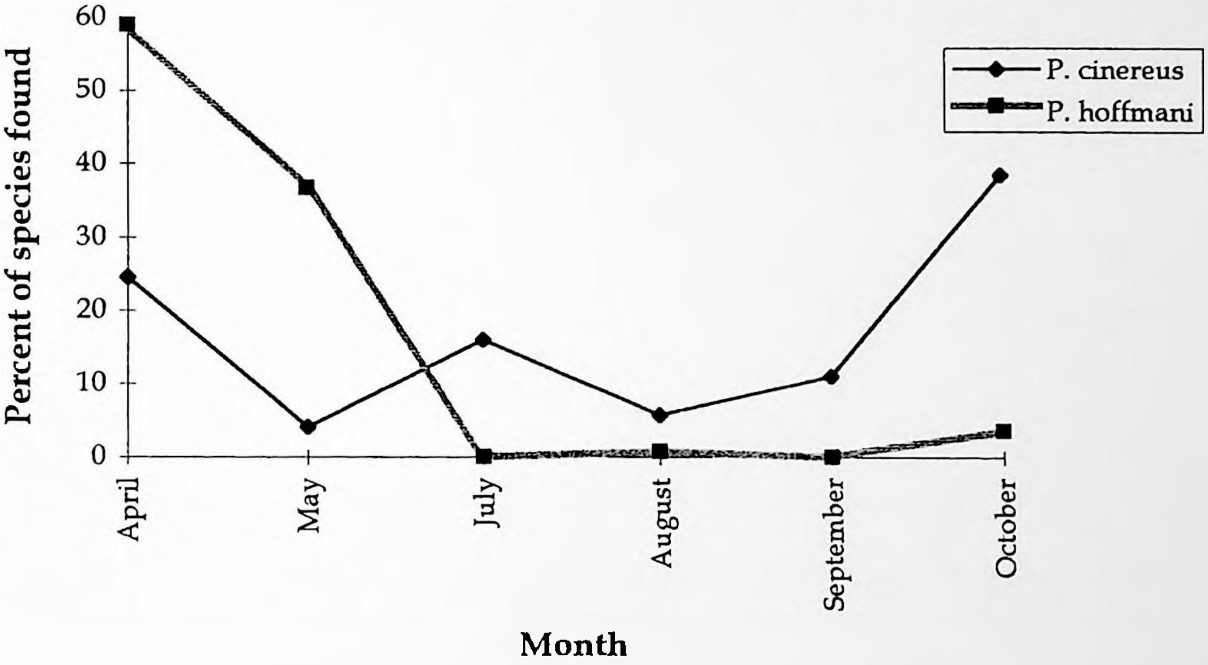
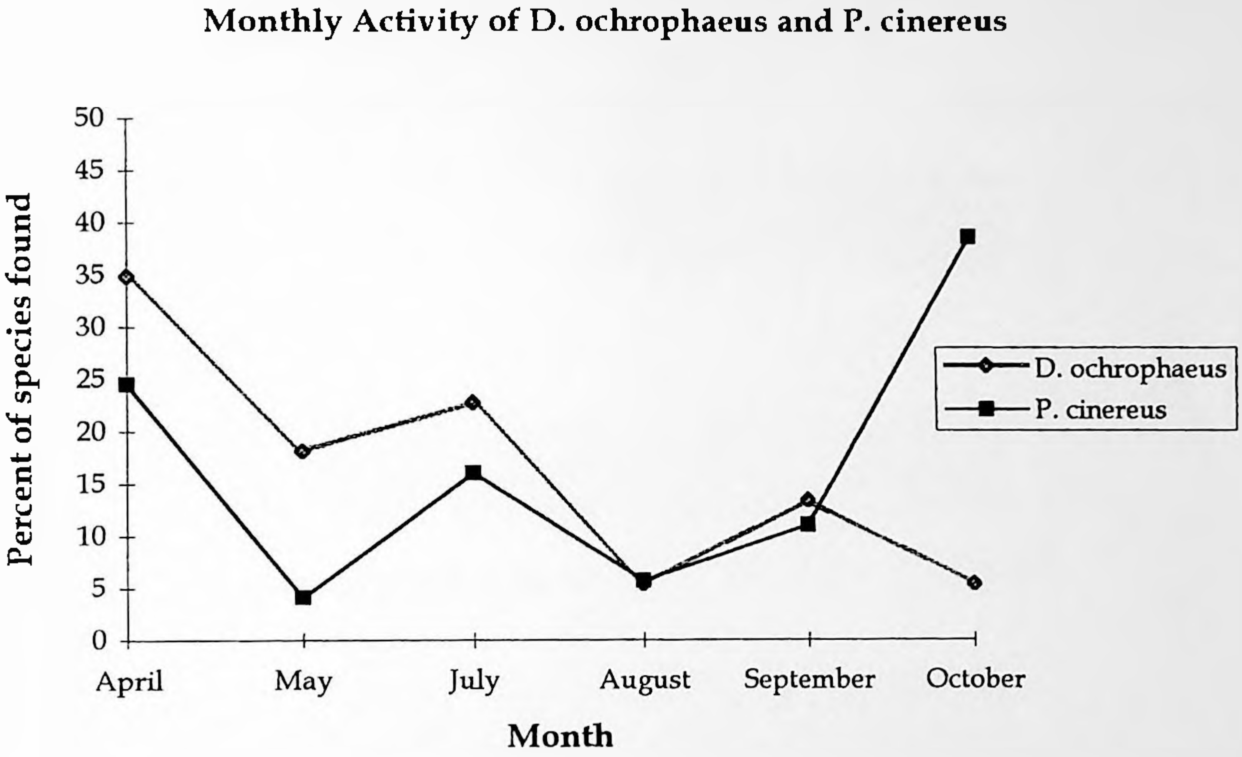


Figure 19. Monthly activity of *P. cinereus* and *P. hoffmani*



Monthly Activity of *P. cinereus* and *P. hoffmani*

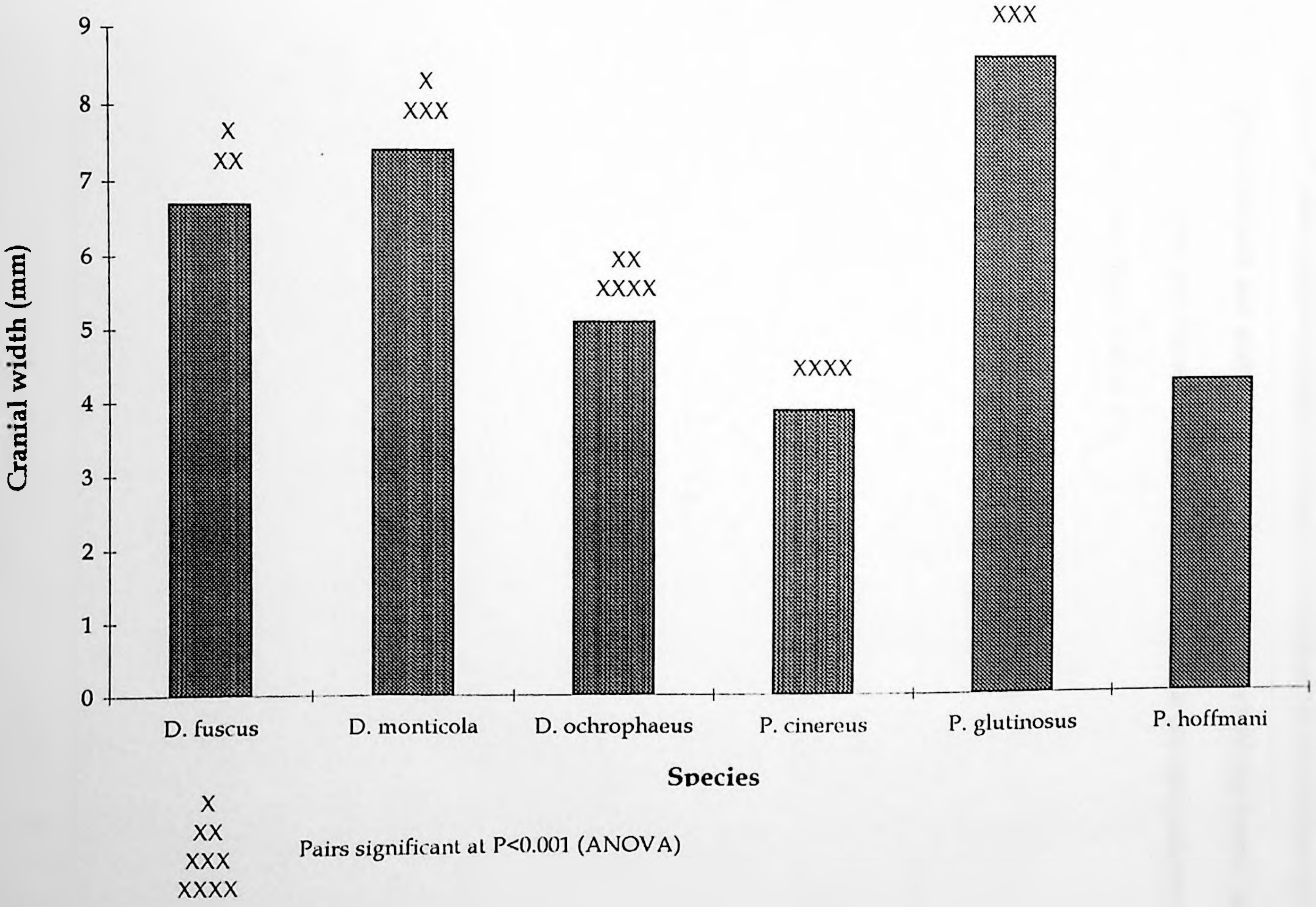
Figure 20. Monthly activity of *D. ochrophaeus* and *P. cinereus*



Monthly Activity of D. ochrophaeus and P. cinereus

Figure 21. Cranial width and prey volume relationship

Average Cranial Width of Salamanders



Environmental parameters

There were no significant differences in the environmental parameters among treatments (Table 10). May had the highest average air temperature and lowest soil pH. June had the highest percent soil and leaf litter moisture. October had the lowest air and soil temperature, lowest soil moisture, highest soil pH and the greatest amount of sunlight reaching the forest floor (Table 11).

Table 10. Average environmental parameters by treatment in 1998.

Treatment	Air Temp (C)	Light (Fc)	Soil Temp (C)	Humidity (%)	Soil Moist (%)	Soil pH	Litter Moist (%)
Bt	21.3	182.6	19.5	73.4	29.5	5.6	21.0
No Treatment	19.1	340.5	19.9	56.9	47.6	5.9	16.7
Gyp	23.0	279.8	19.8	65.3	42.6	5.6	15.9

Table 11. Average environmental parameters by month in 1998

Month	Air Temp (C)	Light (Fc)	Soil Temp (C)	Humidity (%)	Soil Moist (%)	Soil pH	Litter Moist (%)
May	23.8	218.5	19.8	60.8	44.0	4.35	19.08
June	17.1	182.5	17.5	86.6	65.6	4.97	25.77
July	21.8	230.5	20.0	77.5	53.6	4.56	14.96
August	22.8	239.3	20.5	61.0	37.8	4.90	26.46
Sept/Oct	15.5	373.7	15.5	87.7	27.1	5.45	13.65

Discussion

The classical approach to salamander dietary analysis is the examination of prey taxa (Anderson and Martino, 1967; Barbour and Lancaster, 1946; Canterbury and Pauley, 1990; Horn, 1966; Keen, 1979; Marcum, 1994; Petranka, 1984; Stewart and Sandison, 1972). However, the great diversity of insects requires prey items to be identified to broad taxonomic categories, usually order, for diet composition.

Insects within an order are extremely variable in size. Adult coleopterans in North America range in size from less than one millimeter to over 75 mm in length (Borror et al., 1989). Larvae of the same species differ greatly between instars and adults, which results in one species that occupies several size categories throughout its development. Conversely, species of different orders can be the same size. Because of this large variation of insects, use of prey taxa alone is not sufficient in determining dietary overlap.

The studies which used prey taxa to identify feeding niche overlaps found that salamanders are euryphagous predators and select prey based on size. The size of prey taken is dependent on the size of the salamander: larger salamanders take larger prey than do smaller salamanders (Burton,1976;.Mills and Pauley, 1992; Parker, 1994). The relationship between predator and prey size has also been demonstrated in lizards (Vitt et al., 1997; Vitt and Zani, 1996a,b) and is shown in the predator-prey relationship found in this study. This relationship makes it essential to consider prey size, as well as prey taxa, to examine salamander diets and feeding niches.

Jaeger (1990) placed prey into categories based on size. He found that during wetter months (spring), when prey items were more abundant, *P. cinereus* was more apt to consume a wide variety of prey sizes. In drier months, prey items were more scarce and *P. cinereus* preyed on larger items. In this study, Jaeger concluded that when prey items are in short supply, energy is budgeted more efficiently by consuming larger insect prey, which have a lower chitin to body ratio. Jaeger's study provided support for two theories: 1) optimal prey would be those with higher net energy profit per unit of digestion time (Jaeger and Barnard, 1981) and, 2) decreased density of prey items during drier months increases potential for competition (Jaeger 1972, 1980).

These studies suggest that if prey items are reduced in numbers by either environmental conditions (drought/defoliation), or anthropological causes (pesticide applications), salamanders will prey upon larger items and competition for food will increase.

Intraspecific comparisons: treatments / pre- and post-treatment years

I did not find a change in the diets of *P. cinereus* and *D. ochrophaeus* between treatment and post-treatment years (1997 and 1998). Data from the insect portion of the LTGM study available at the time of this thesis, found no affect of *Bt* on formicids but did find that *Bt* significantly reduced the number of larval lepidopterans within the first month of treatment.

Although comprehensive data of insect diversity and abundance on the plots were not available, formicid and lepidopteran data suggest there was no effect on the primary prey items of salamanders due to *Bt*.

I did not find a correlation of salamander diets between pre-treatment and post-treatment years on either the *Bt* or no treatment plots, which implies that the diets differ before and after treatment. I did, however, find a correlation for *D. ochrophaeus* on Gypchek plots before and after treatments. Gypchek served as the positive control for this study since it does not impact any non-target organisms and controls gypsy moth defoliation by inhibiting larval development.

This data conflicts with comparisons made between treatments. Comparisons between treatments indicate that there is no difference between *Bt*, Gypchek or no treatment plots after treatments were applied. Pre- and post-treatment year data indicated that salamander diets change after *Bt* applications. However, these data also indicate that salamander diets changed before and after treatment years on plots which received no treatments. No-treatment plots were not sprayed by pesticides, but also did not experience drastic gypsy moth defoliation.

This study was designed to test the effects of *Bt* and gypsy moth defoliation on non-target insects, birds and salamanders. However, since gypsy moth defoliation did not occur, the no-treatment plots served as a secondary control for the effects of *Bt* applications. Furthermore, since pre-/post-treatment year food data showed no correlation between salamander diets on plots which did not receive pesticide application or defoliation, I do not have evidence to suggest salamander diets changed before and after *Bt* applications.

The significant correlation and trends seen in the diets of *D. ochrophaeus* and *P. cinereus* between treatments for both prey taxa and prey size shows that diets did not differ between plots for either species. Based on these results there is no evidence to support that the *Bt* applications affected salamander food selection.

Interspecific comparisons

Since there were no differences in the diets of *D. ochrophaeus* or *P. cinereus* between plots, I pooled food data from all plots in both 1997 and 1998 for each species to determine feeding niche overlaps. Field studies conducted for the salamander portion of the LTGM project have shown that there is no difference in surface abundance of salamanders found on different treatment plots. Based on these results, I pooled these field data from all plots in 1997 and 1998 to determine habitat, daily activity and monthly activity of each species. Pooling data for both diet and field analysis produced large sample size of each species.

Five feeding niche overlaps occurred based on prey taxa, prey size and habitat. *Desmognathus ochrophaeus* was found in equal numbers in aquatic and terrestrial habitats and has feeding niche overlaps with both *D. fuscus* and *P. cinereus.* Aquatic and terrestrial habitats will be discussed separately with *D. ochrophaeus* presented as a link between these two habitats.

Aquatic habitats: *D. fuscus Vs D. monticola*

Based on prey taxa, prey size, habitat and monthly activity, feeding niche overlaps exist between *D. monticola* and *D. fuscus.* However, the time of day these species were found differed. Only 10 percent of *D. fuscus* were found at night compared to 63 percent of *D. monticola*. These percentages represent when salamanders were found and do not confirm time of foraging.

Daily activity data can be supported as foraging time by examination of the food items of each species. The diet of *D. monticola* was 53 percent adult dipterans. The upper jaw of *Desmognathus* species is designed to flip up, as opposed to the lower jaw flipping down. This morphology functions to allow these salamander to efficiently catch flying insects (Zug, 1993). Terrestrial salamanders of the genus *Plethodon* do not have this jaw structure and all contained less than 5 percent flying insects in their diets. A salamander would have to expose itself on top of rocks and leaf litter in order to catch flying insects and would be at a disadvantage to forage in this manner during the day. All *D. monticola* found at night were found perched on top of rocks in streams and have been observed capturing flying insects in this manner (pers. obs.).

Desmognathus fuscus, which was found less frequently at night, contained only 28 percent adult dipterans in its diet. Another 29 percent of its diet was composed of coleopterans (Carabidae, Chrysomelidae and Curculionidae) and formicids, insects ncountered under rocks and logs. These differences in diets may be reflective of different daily foraging activity. *Desmognathus fuscus* was found less frequently at night and contained less flying insects than *D. monticola*. These differences may also reduce competition for food between these two species.

Although these species occupy the same habitat, only one species was dominant in each study stream. In streams on plots 11, 12 and 13, *D. monticola* was the dominant species (total 66 *D. monticola*, 20 *D. fuscus*). *Desmognathus fuscus* was common on streams 16, 17, and 18 (total 26 *D. fuscus*, 1 *D. monticola*) where few *D. monticola* were found. Given the strong feeding niche overlap between these species, the absence or reduced abundance of one species in the presence of the other suggests competitive exclusion is occurring between them.

Aquatic to Terrestrial Habitats: *D. ochrophaeus* vs. *D. monticola*
D. ochrophaeus vs. *D. fuscus*
D. ochrophaeus vs. *P. cinereus*

All streams contained *D. ochrophaeus*. I did not find a dietary overlap between *D. monticola* and *D. ochrophaeus*. However, *D. ochrophaeus* was found more often on the banks and floodplain than within the streams where *D. monticola* was found. Hairston (1986) suggested that predation was the most common interaction between these two species. He found that removal of *D. ochrophaeus* caused a decrease in numbers of *D. monticola*. Only two salamanders were found in *D. monticola* diets (< 0.5%), both of which were identified as *D. monticola* subadults. Although this confirms that *D. monticola* preys on salamanders, the small proportion of salamanders in the diet does not imply that salamanders are their primary food source. Although predation may be one reason for the niche partitioning of *D. monticola* and *D. ochrophaeus*, it is probably not the primary reason in these study areas.

There may be feeding niche overlaps between adult *D. ochrophaeus* and subadult *D. monticola*. This study only examined the diets of adults, in which there were no overlaps between these two species. However, average SVL of adult *D. monticola* (53mm) is considerably larger than adult *D. ochrophaeus* (33mm). Since the size of prey taken is dependent on the size of the salamander, this difference in adult size may prevent these species from competing for food as adults. However, subadult *D. monticola* average 38.2 mm in size (Pauley and Raimondo, unpub. data), which is statistically similar to adult *D. ochrophaeus* (t-test, $p = 0.05$).

I found a feeding niche overlap between *D. fuscus* and *D. ochrophaeus*. Plots 16, 17 & 18, which were heavily populated with *D. fuscus*, contained *D. ochrophaeus* within the stream as well as on the floodplain and terrestrial habitats. I did not find any evidence of niche partitioning or competitive exclusion where these species coexisted.

Keen (1982) found that interspecific competition influenced spatial distribution of desmognathinae salamanders. He found that smaller salamanders shifted from established habitats when larger species were introduced. Larger species of plethodontid salamanders are more aggressive and physically dominate smaller species (Thurow, 1975; Keen and Sharp, 1984; Townsend and Jaeger, 1998). Aggression of larger species may allow them to establish territories in optimal habitats with greater access to prey (Mathis 1990).

Desmognathus ochrophaeus was the smallest species in this study and the most terrestrial desmognathinae salamander. Territoriality and aggression of the two larger congeners may explain the movement of *D. ochrophaeus* to more terrestrial habitats.

Desmognathus ochrophaeus had the largest habitat breadth of all species, being found equally in aquatic and terrestrial habitats. It was also the only species which had feeding niche overlaps with both aquatic and terrestrial species. Feeding niche overlaps were found between *D. ochrophaeus* and *P. cinereus* on the basis of prey taxa, prey size and habitat. Daily and monthly activities of these two species were also very similar. The majority (> 70%) of both species were found during the day investigations. Although 40 percent of *P. cinereus* and only 5 percent of *D. ochrophaeus* were found in October, activity from April - September is similar for both species.

Habitat and dehydration tolerances determine the most terrestrial and most aquatic species: *D. monticola* is the most aquatic, *P. hoffmani* is the most terrestrial.

Using this information, I have created a terrestrial-aquatic continuum of salamander food resources. Aquatic salamanders have large percentages of adult dipterans in their diets. This percentage decreases linearly with salamanders occupying more terrestrial habitats. *Plethodon hoffmani*, the most terrestrial species, did not contain any adult dipterans in its diet. All but approximately 10 percent of the dipterans removed from the stomachs were digested too completely to be identified to family. However, those that were identifiable were in the family Chironomidae, which are mostly found swarming over bodies of water (Borror et al., 1992).

Conversely, diets of terrestrial salamanders contain large numbers of formicids and Acari in their diets, which decrease in salamanders occupying aquatic habitats. Acari were not identified to family, but were identified as not belonging to the sub-cohort Hydrachnidia. In North America, 95 percent of aquatic mite species and 95 percent of aquatic mites encountered belong to this group (Peckarsky et al., 1990). Aquatic salamanders possessed less than 4.0 percent Acari in their diets.

As an occupant of both habitats, *D. ochrophaeus* contains an intermediate percentage of adult dipterans, formicids and Acari (16%, 14% and 21%, respectively). These data are the first to demonstrate a distinct separation of food resources of salamanders from aquatic to terrestrial habitats.

Terrestrial habitats: *P. cinereus Vs. P. glutinosus*
P. cinereus Vs. P. hoffmani

The feeding niche overlap between *P. cinereus* and *P. glutinosus* is similar to that described for *D. fuscus* and *D. monticola*. Species shared overlaps in prey taxa, prey size and habitat, but daily activity differed between them. Only 22 percent of *P. cinereus* were found during night investigations where 60 percent of *P. glutinosus* were found at these times. These species were frequently found within 10 meters of each other along the same night transect. On one day investigation, I observed three *P. cinereus* and two *P. glutinosus* under the same coverboard site foraging on a colony of ants. Since *Plethodon* species are under cover objects during the day, distinction between day and night foraging can not be determined in the scope of this study.

Feeding niche overlaps were also found between *P. cinereus* and *P. hoffmani.* These species contained similar food, habitat, daily activity, and were frequently found under the same board sites. However, a distinct difference in the monthly activity of these two species reduces their competition for resources. *Plethodon hoffmani* was abundantly found on the surface of the forest floor during April and May (97% of all encountered). From June through September only one *P. hoffmani* was found. *Plethodon cinereus* was found throughout the whole year, with the highest numbers found in October. These differences in monthly activity show these two species avoid competition by being active at different times of the year.

Summary

Salamander diets are not only indicative of species habitat and interspecific interactions, but can be used as indicators of changes in the food web. Studies of salamander diets gave no indication that the gypsy moth pesticide, *Bt,* has impacted the food of salamanders in West Virginia. If diet shifts had been detected as a result of pesticide treatments, actions could have been made to curb the use of those pesticides before large scale impacts occur.

The interspecific diet analyses confirm interactions between species which have been seen by many investigators but which have not been examined for the six species described here. Food partitioning between aquatic and terrestrial salamanders may represent the first aquatic / terrestrial continuum of salamander food resources. Daily and monthly activities as well as habitat overlaps have also contributed to our knowledge of the ecology of six species found within the Monongahela National Forest, West Virginia.

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