DIET OF THE DEL NORTE SALAMANDER (*PLETHODON ELONGATUS*): DIFFERENCES BY AGE, GENDER, AND SEASON

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ABSTRACT—Terrestrial salamanders are integral components of forest ecosystems and the examination of their feeding habits may provide useful information regarding various ecosystem processes. We studied the diet of the Del Norte Salamander (*Plethodon elongatus*) and assessed diet differences between age classes, genders, and seasons. The stomachs of 309 subadult and adult salamanders, captured in spring and fall, contained 20 prey types. Nineteen were invertebrates, and one was a juvenile Del Norte Salamander, representing the first reported evidence of cannibalism in this species. Mites and ants represented a significant component of the diet across all age classes and genders, and diets of subadult and adult salamanders were fairly similar overall. We detected, however, an ontogenetic shift with termites and ants becoming less important and spiders and mites becoming more important with age. These differences between subadults and adults can likely be attributed to the inability of subadults to consume larger prey items due in part to gape limitation. The diet of the Del Norte Salamander, like other plethodontids, consists of a high diversity of prey items making it an opportunistic, sit-and-wait predator.

Key words: Del Norte Salamander, *Plethodon elongatus,* food habits, diet, northern California, southern Oregon

Terrestrial salamanders represent a significant component of vertebrate biomass in forest ecosystems (Burton and Likens 1975a) and strongly influence nutrient dynamics and energy flow (Burton and Likens 1975b). They may play an important role in the regulation of food web dynamics and can greatly impact abundances of soil invertebrates (reviewed by Davic and Welsh 2004). Knowledge of the feeding habits of terrestrial salamanders can provide useful system-specific information on variation in feeding behavior, food availability, prey species diversity, and trophic dynamics.

We examined the diet of the Del Norte Salamander (*Plethodon elongatus*), a species endemic to northern California and southern Oregon (Jones and others 2005; Welsh and Bury 2005). This terrestrial plethodontid salamander is associated with rocky substrates in low-elevation mixed conifer-hardwood forests (Nussbaum and others 1983; Stebbins 2003; Welsh and Bury 2005), and may require ecological conditions found primarily in late seral stage forests (Welsh 1990; Welsh and Lind 1995; Jones and others 2005). However, Diller and Wallace (1994) observed dense populations of Del Norte Salamanders in younger coastal redwood forests and attributed this to the climatic differences between the habitats of coastal and more inland populations.

Prior to June 2002, the Del Norte Salamander was listed as a Survey and Manage Species and protected on federal forestlands under the Northwest Forest Plan (USDA and USDI 1994). Currently it is designated as a Species of Special Concern by the State of California (Jennings and Hayes 1994) and a Species of Concern by the State of Oregon (Marshall 1992). These categories provide limited or no protections. Recent analyses suggest that this species may be comprised of several genetically distinct lineages.

Our objectives were to describe the composition of the Del Norte Salamander diet, to assess differences in diet by age class, gender,

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and season, and to evaluate any differences that might occur based on capture method.

Methods

We captured and collected 309 Del Norte Salamanders from 9 localities in Del Norte, Humboldt, and Trinity counties, California, in 1984 and 1985. We captured 120 salamanders using time-constrained searches (TCS) during spring (March through May) and 189 salamanders using pitfall traps (PF) during fall (October through November). These months corresponded with the time periods when these salamanders were active on the forest floor. On the day of capture, animals were transported to the laboratory where they were euthanized in 0.2% chloretone, fixed in 10% formalin, and stored in 70% ethanol. We measured snout-vent length (SVL) and total length to the nearest 1 mm and mass to the nearest 0.1 g for each euthanized specimen.

In the laboratory, stomachs were removed and contents were examined in ethanol using a 10x dissecting microscope. We examined the stomach contents of all salamanders captured: 126 males, 116 females, and 67 subadults-juveniles. Gender and age class of specimens were determined by dissection using maturity and condition of sex organs as indicators (see Ollivier and Welsh 2003). We combined juvenile and subadult data (hereafter subadults) to obtain sufficient sample sizes. Because we could not determine the gender of juvenile animals, we did not examine differences in diet between subadult males and females. We sorted and identified all prey items to order, or family when possible (Table 1), counted each prey item, and measured the length, width, and depth of intact items of each prey type in a given specimen.

We determined the number (total number of a given prey type in a stomach), frequency (number of stomachs that contained each prey type), volume, and importance of each prey type by season for all salamanders, each age class, and adults of each gender. Volume of prey type was calculated as $V = n \times l \times w \times d$, where n = number, l = prey length, w = prey width, and d = prey depth. We calculated the importance value (I_x) for each prey type using the following equation (Anderson and Mathis 1999):

TABLE 1. Common names for organisms in prey types.

Prey type	Common name
Araneae	Spiders
Chilopoda	Centipedes
Coleoptera	Beetles
Collembola	Springtails
Diplopoda	Millipedes
Diplura	Diplurans
Diptera	Flies
Formicidae (Order Hymenoptera)	Ants
Gastropoda	Snails and Slugs
Hymenoptera (except Formicidae)	Bees, Wasps, and Sawflies
Isopoda	Isopods
Isoptera	Termites
Ixodidae (Order Acari)	Ticks
Lepidoptera	Butterflies and Moths
Oligochaeta	Earthworms
Orbatidae (Order Acari)	Mites
Orthoptera	Grasshoppers, Crickets, and Katydids
Plethodon elongatus (Order Amphibia)	Del Norte Salamander
Pseudoscorpiones	Pseudoscorpions
Trichoptera	Caddisflies

$$I_x = \frac{(n_x/N) + (v_x/V) + (f_x/F)}{3}$$

where n_x = number of a given prey type, N = sum of numbers of all prey items, v_x = volume of a given prey type, V = sum of volumes of all prey items, f_x = frequency of a given prey type, and F = sum of frequencies of all prey items. The importance value is an index that provides a more complete analysis of an organism's food habits by incorporating numbers, volumes, and frequencies of prey types (Powell and others 1990; Anderson and Mathis 1999).

Cumulative prey curves were constructed for each group to determine if adequate sample sizes were obtained to describe the diet and differences between age classes, genders, and seasons (Adams and Kay 2002). To generate curves, the order in which stomachs were analyzed was randomized 100 times and the mean number of new prey species cumulated consecutively was plotted against the number of stomachs examined. An asymptotic relationship was considered to be an indication that a sufficient number of stomachs were analyzed to represent dietary habits (Cailliet and others 1986).

We calculated prey richness (number of spe-

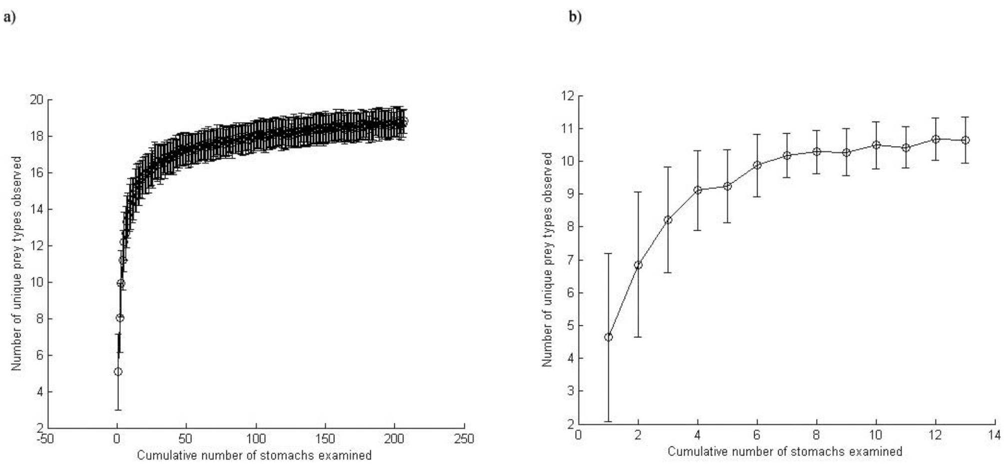

FIGURE 1. Cumulative prey curves for a) all salamander stomachs (n = 207) containing identifiable prey items, representing the largest sample, and b) subadults collected in the fall (n = 13), representing the smallest sample. Error bars denote standard deviations. Asymptotic cumulative prey curves for other groups are not shown.

cies), prey evenness (equitability of species), and Shannon index of prey diversity (a diversity index that accounts for both evenness and species richness) by season, age class, and gender (Magurran 1988). We compared diversity of prey species between groups using t-tests (Magurran 1988) (α = 0.017 after Bonferroni adjustment). This allowed us to examine the possible effects of capture method, season, and age class on diet diversity. We used t-tests to compare prey volume and number of prey items between age classes, genders, and seasons (α = 0.017 after Bonferroni adjustment). Prey volume and number of prey items were log-transformed prior to analysis.

RESULTS

Prey Items

Asymptotic cumulative prey curves indicated that an adequate number of stomachs were examined to comprehensively describe and compare food habits of all groups (Fig. 1a and 1b). Of 309 specimens, the stomachs of 218 (71%), comprised of 160 adults and 58 subadults, contained at least 1 prey item or other unidentifiable matter. Of these, 207 contained identifiable prey items. Ninety-one specimens (29%) had empty stomachs, with nearly all (97%) of these being captured in the fall in pitfall traps. Thirty-six percent of subadults and 48% of adults had empty stomachs in the fall, compared with 2% and 3%, respectively, in the spring.

Specimen stomachs contained a total of 2449 identifiable prey items (Table 2) representing 20 prey types (19 invertebrate and 1 vertebrate). The mean number of prey items per salamander, for all age classes combined, was higher in the spring ($\bar{x}$ = 13.7, s = 24.5) than in the fall ($\bar{x}$ = 4.5, s = 17.0). Much of this difference between seasons was attributable to subadults. The number of adult stomachs that contained contents was comparable between the two seasons (spring: n = 73; fall: n = 77), with approximately 700 prey items observed in both the spring and fall. However, the number of subadult stomachs that contained contents was not comparable between seasons (spring: n = 13; fall: n = 44). Approximately 3 times more prey items were observed in the spring than in the fall after correcting for the number of stomachs sampled (Table 2). Adult males contained almost twice as many prey items in the fall as adult females.

We found differences in number of prey items between age classes and seasons. Adult salamanders had significantly fewer combined (fall and spring) mean number of prey items ($\bar{x}$ = 9.5, s = 18.5) than subadults ($\bar{x}$ = 18.4, s = 34.2) (t = 3.37, df = 205, $P < 0.001$). The mean number of prey items found in the stomachs of all salamanders captured in spring ($\bar{x}$ = 14.2, s

TABLE 2. Results of the examination of stomach contents by season, age class, gender and 3 measures of prey species diversity. See Magurran (1985) for calculation of diversity and evenness.

Category	n	Total number empty stomachs	Total number prey items	Total prey volume (mm^3)	Richness	Diversity (H')	Evenness
Fall	178	88	806	4456	16	2.510	0.905
Subadult	21	8	111	536	12	2.333	0.939
Adult	157	80	695	3920	16	2.492	0.899
Male adult	80	38	458	2218	16	2.509	0.905
Female adult	77	42	237	1702	14	2.397	0.908
Spring	120	3	1643	3327	19	2.583	0.877
Subadult	45	1	920	592	16	2.524	0.910
Adult	75	2	723	2735	19	2.592	0.880
Male adult	43	2	421	1082	17	2.573	0.908
Female adult	32	0	302	1653	17	2.535	0.895

$= 24.7$) was significantly greater than in fall ($\bar{x} = 9.0$, $s = 23.1$) ($t = -5.33$, $df = 205$, $P < 0.001$). There was no significant difference in mean number of prey items between adult males ($\bar{x} = 10.6$, $s = 23.7$) and females ($\bar{x} = 8.0$, $s = 8.0$) ($t = -0.06$, $df = 148$, $P = 0.950$).

We found no significant differences in mean prey volume between combined (fall and spring) adults ($\bar{x} = 44.3$, $s = 76.0$) and subadults ($\bar{x} = 19.8$, $s = 39.9$) ($t = -2.05$, $df = 205$, $P = 0.042$), between all salamanders captured in spring ($\bar{x} = 28.3$, $s = 58.6$) and those captured in fall ($\bar{x} = 49.5$, $s = 79.0$) ($t = 1.07$, $df = 205$, $P = 0.285$) or between adult males ($\bar{x} = 39.6$, $s = 74.4$) and females ($\bar{x} = 50.1$, $s = 78.2$) ($t = 1.07$, $df = 148$, $P = 0.286$).

The most sizeable prey items were observed in adult specimens. The largest (405 mm^3) and longest (72 mm) prey observed was an earthworm (Oligochaeta) found in an adult female. The widest prey item was an 8 mm-wide spider (Araneae) observed in an adult male. The largest (231 mm^3) and widest (3.8 mm) prey item observed in a subadult was a gastropod (Gastropoda). The longest prey item observed in a subadult was a 27.8 mm-long centipede (Chilopoda). The sole vertebrate prey item, an 18 mm juvenile Del Norte Salamander, was found in the stomach of an adult male captured in the fall.

Analysis of Diet

Diversity.—Indices of diversity for prey species composing the diet of Del Norte Salamanders are reported in Table 2. We identified 16 prey types in the fall and 19 in the spring. Prey species richness was less for subadults than adults in both seasons (Table 2). There were no significant differences in prey diversity between seasons when all age classes were combined ($t = 1.52$, $df = 505$, $P = 0.129$) or when age classes were tested separately (adults: $t = 1.73$, $df = 460$, $P = 0.084$; subadults: $t = 2.43$, $df = 64$, $P = 0.018$). There were no differences in prey diversity between age classes when both seasons were combined ($t = 2.27$, $df = 564$, $P = 0.024$) or when seasons were tested separately (spring: $t = 1.24$, $df = 486$, $P = 0.216$; fall: $t = 1.97$, $df = 70$, $P = 0.053$). There also were no differences in prey diversity between genders when both seasons were combined ($t = 0.76$, $df = 468$, $P = 0.450$) or when seasons were tested separately (spring: $t = 0.54$, $df = 276$, $P = 0.589$; fall: $t = 1.33$, $df = 194$, $P = 0.185$). Evenness values were similar for all categories and close to 1 (Table 2).

Composition.—The Del Norte Salamander has a broad diet that, in our study, was composed of 20 different prey types, including an instance of cannibalism (Tables 3 and 4). Mites (Oribatidae) and ants (Formicidae) represented an important component of the diet across all age classes and genders. Although the diets of subadult and adult salamanders were fairly similar overall, we detected an ontogenetic shift in the spring sample with termites (Isoptera) and ants (Formicidae) decreasing in importance and spiders (Araneae) and mites (Oribatidae) increasing in importance with age (Table 3). The overall importance values of the 8 most frequent prey types for subadult and adult salamanders are shown in Figure 2. In subadults, 4 of 16 prey types had the highest importance values (representing 50% of prey

TABLE 3. Diet composition of Del Norte Salamanders captured in spring using time constrained searches. n = total number of a given prey type found in the stomach of a salamander. f = number of salamander stomachs containing the prey item. v = prey volume. I = importance value. Order Hymenoptera does not include formicids. Formicidae was analyzed as a separate prey type.

	All salamanders				Subadults				Adults				Adult females				Adult males			
Prey type	n	f	v	I	n	f	v	I	n	f	v	I	n	f	v	I	n	f	v	I
Araneae	55	41	483	0.09	18	13	27	0.04	37	28	456	0.10	14	12	113	0.07	23	16	343	0.15
Chilopoda	21	20	512	0.07	5	5	40	0.03	16	15	473	0.08	9	8	356	0.10	7	7	116	0.05
Coleoptera	52	38	363	0.07	18	18	58	0.07	34	20	305	0.08	13	9	192	0.08	21	11	113	0.07
Collembola	255	72	181	0.12	125	29	95	0.15	130	43	86	0.12	68	18	40	0.13	62	25	46	0.11
Diplopoda	24	16	293	0.04	13	7	39	0.04	11	9	254	0.05	5	4	124	0.04	6	5	130	0.05
Dipluran	68	24	129	0.04	46	9	15	0.04	22	15	114	0.04	11	9	105	0.06	11	6	9	0.02
Diptera	72	41	151	0.06	31	15	25	0.05	41	26	126	0.06	18	11	26	0.05	23	15	100	0.08
Formicidae	344	45	397	0.14	177	19	180	0.20	167	26	218	0.13	66	10	80	0.12	101	16	138	0.15
Gastropoda	12	8	5	0.01	5	3	1	0.01	7	5	4	0.01	1	1	0	0.00	6	4	4	0.01
Hymenoptera	8	6	14	0.01	2	1	1	0.00	6	5	13	0.01	2	1	4	0.01	4	4	9	0.01
Isopoda	29	16	88	0.03	13	7	5	0.02	16	9	84	0.03	7	3	61	0.03	9	6	22	0.03
Isoptera	301	38	79	0.09	246	17	57	0.15	55	21	22	0.05	18	9	10	0.05	37	12	12	0.06
Ixodidae	34	20	7	0.02	19	11	6	0.03	15	9	1	0.02	0	0	0	0.00	15	9	1	0.03
Lepidoptera	1	1	13	0.00	0	0	0	0.00	1	1	13	0.00	0	0	0	0.00	1	1	13	0.01
Oligochaeta	1	1	450	0.05	0	0	0	0.00	1	1	450	0.06	1	1	450	0.09	0	0	0	0.00
Oribatidae	221	75	54	0.10	88	28	20	0.09	133	47	35	0.12	55	19	16	0.11	78	28	18	0.12
Orthoptera	77	2	35	0.02	76	1	9	0.03	1	1	26	0.00	1	1	26	0.01	0	0	0	0.00
Plethodon elongatus	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00
Pseudoscorpiones	65	38	42	0.04	38	22	15	0.06	27	16	27	0.03	11	8	20	0.04	16	8	7	0.03
Trichoptera	3	3	30	0.01	0	0	0	0.00	3	3	30	0.01	2	2	29	0.01	1	1	1	0.00
Empty	—	3	—	—	—	1	—	—	—	2	—	—	—	0	—	—	—	2	—	—

TABLE 4. Diet composition of Del Norte Salamanders captured in fall using pitfall traps. n = total number of a given prey type found in the stomach of a salamander. f = number of salamander stomachs containing the prey item. v = prey volume. I = importance value. Order Hymenoptera does not include formicids. Formicidae was analyzed as a separate prey type.

	All salamanders				Subadults				Adults				Adult females				Adult males			
Prey type	n	f	v	I	n	f	v	I	n	f	v	I	n	f	v	I	n	f	v	I
Araneae	58	34	984	0.14	14	5	180	0.20	44	29	804	0.14	29	17	376	0.18	15	12	428	0.11
Chilopoda	11	8	402	0.05	0	0	0	0.00	11	8	402	0.05	5	3	180	0.05	6	5	222	0.05
Coleoptera	63	24	489	0.10	3	2	28	0.04	60	22	461	0.10	15	7	38	0.06	45	15	422	0.14
Collembola	38	16	16	0.04	11	5	3	0.08	27	11	13	0.03	16	6	8	0.05	11	5	5	0.02
Diplopoda	29	15	727	0.09	3	1	22	0.03	26	14	706	0.10	19	7	508	0.15	7	7	198	0.06
Dipluran	76	10	25	0.05	8	2	4	0.04	68	8	21	0.05	61	5	17	0.11	7	3	4	0.01
Diptera	45	25	117	0.06	6	3	23	0.06	39	22	95	0.06	15	9	41	0.06	24	13	53	0.06
Formicidae	80	17	171	0.07	27	4	24	0.13	53	13	146	0.06	11	6	34	0.04	42	7	112	0.07
Gastropoda	9	6	297	0.03	1	1	231	0.16	8	5	66	0.02	2	1	2	0.01	6	4	64	0.03
Hymenoptera	1	1	3	0.00	0	0	0	0.00	1	1	3	0.00	0	0	0	0.00	1	1	3	0.00
Isopoda	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00
Isoptera	17	8	5	0.02	1	1	0	0.01	16	7	5	0.02	1	1	1	0.01	15	6	4	0.03
Ixodidae	29	16	4	0.03	12	4	2	0.07	17	12	3	0.03	7	5	1	0.03	10	7	2	0.03
Lepidoptera	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00
Oligochaeta	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00
Oribatidae	104	39	36	0.10	14	6	7	0.10	90	33	29	0.10	33	13	11	0.10	57	20	18	0.10
Orthoptera	232	14	1005	0.19	0	0	0	0.00	232	14	1005	0.22	22	7	485	0.15	210	7	520	0.25
Plethodon elongatus	1	1	161	0.01	0	0	0	0.00	1	1	161	0.02	0	0	0	0.00	1	1	161	0.03
Pseudoscorpiones	13	5	14	0.01	11	3	13	0.07	2	2	1	0.00	1	1	0	0.01	1	1	0	0.00
Trichoptera	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0	0	0.00
Empty	—	88	—	—	—	8	—	—	—	80	—	—	—	42	—	—	—	38	—	—

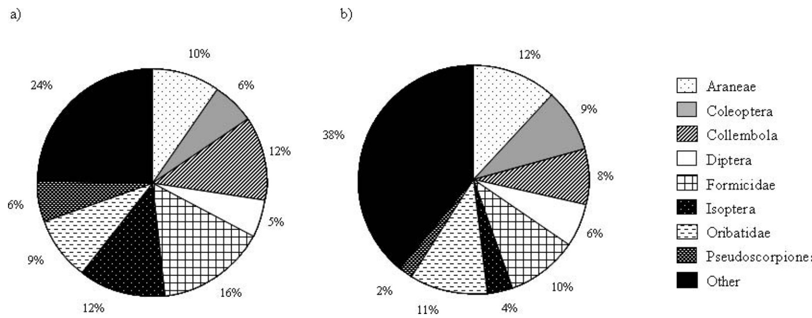

FIGURE 2. Importance values as percentages, for fall and spring samples combined, of the 8 most frequent prey types in a) subadults and b) adults. All other prey types are grouped into the category labeled ''Other.''

importance): ants (Formicidae), termites (Isoptera), springtails (Collembola), and spiders (Araneae) (Fig. 2a). In adults, 5 of 19 prey types had the highest importance values (representing 50% of prey importance): spiders (Araneae), mites (Oribatidae), ants (Formicidae), beetles (Coleoptera), and springtails (Collembola) (Fig. 2b).

In the spring sample, 5 prey types had the highest importance values for all salamanders (Table 3). Of these taxa, ants (Formicidae), mites (Oribatidae), and springtails (Collembola) were important across all groups (Table 3). In addition, termites (Isoptera) were important for subadults and spiders (Araneae) were important for adults, especially for males (Table 3).

In the fall sample, 8 prey types had the highest importance values for all salamanders (Table 4). Spiders (Araneae) and mites (Oribatidae) were important across all groups (Table 4). Ants (Formicidae) and snails and slugs (Gastropoda) were important prey items for subadults (Table 4). Crickets and katydids (Orthoptera) were important for all adults, regardless of gender (Table 4). Millipedes (Diplopoda) and diplurans were important for adult females, and beetles (Coleoptera) were important for adult males.

DISCUSSION

Comparing the diversity or number of prey items in diets among different salamander species can be challenging because researchers categorize prey items differently. In our study, prey items were distributed between 18 orders. However, we divided the Hymenoptera into 2 categories, ants (Family Formicidae) and other Hymenoptera, and the Order Acari into 2 groups, ticks in the Family Ixodidae and mites in the Family Oribatidae, in order to distinguish these apparently important groups of prey. We also identified the only vertebrate prey item, the Del Norte Salamander, to species. Other researchers have generally identified prey items to Order, so for the sake of comparison we will discuss the 18 prey types (Orders) that we observed in the diet of the Del Norte Salamander.

The food habits of the Del Norte Salamander were first described by Bury and Johnson (1965). They examined the stomach contents of 24 adult salamanders collected in winter (December and January) in northern California and observed a total of 10 prey types. Nine of the prey types were similar to those observed in our study, whereas prey in the Order Hemiptera (true bugs) were not represented in our diet analysis. They found that beetles and springtails were the most numerous and frequent prey consumed by adult salamanders in winter. In our study, beetles were moderately numerous and frequent, and had relatively high importance values in spring and fall for adult Del Norte Salamanders (Tables 3 and 4). Springtails were numerous and frequent and had relatively high importance values only in spring (Table 3). We also found that ants, mites, and springtails were the most numerous, and mites and springtails were the most frequent prey items collected from the stomachs of adult salamanders in spring (Table 3). In fall, Orthopterans and mites were the most numerous, and mites and spiders were the most frequent prey items in adult salamander stomachs (Table 4). In both seasons, ants and orthopterans had the highest importance values, respectively (Tables 3 and 4). Discrepancies between this study and Bury and Johnson (1965) may be a result of differences in sample size or sampling season.

Researchers have evaluated the diets of other terrestrial salamanders in the genus *Plethodon* from the eastern and western U.S. In the eastern U.S., the number of prey types in diets was 13 in the Northern Slimy Salamander (*P. glutinosus*) (Powders and Tietjen 1974), 14 in the Jordan's Redcheek Salamander (*P. jordani*) (Powders and Tietjen 1974), and 12–19 in 3 separate studies of the Northern Redback Salamander (*P. cinereus*) (Jameson 1944; Jaeger 1972; Burton 1976). The number of prey types in diets of western species was 12 in the Western Redback Salamander (*P. vehiculum*) and 15 in the Dunn's Salamander (*P. dunni*) (Dumas 1956). The Northern Slimy Salamander expressed the highest diversity in diet ($H' = 3.117$, $n = 40$) (Powders and Tietjen 1974) and the Western Redback Salamander expressed the lowest diversity ($H' = 1.695$, $n = 37$) (Dumas 1956). The diet of the Del Norte Salamander is quite broad compared to these species, with 18 prey types and a high prey item diversity ($H' = 2.583$, $n = 207$). In addition, the diet of this salamander had high prey evenness values (0.880–0.939). These results suggest that this species is a generalist predator (*sensu* Jaeger 1981).

We observed seasonal differences in the diet of the Del Norte Salamander. Spring specimens contained 3 times more prey items per salamander than fall specimens. Much of this difference was attributable to subadults, with 13 stomachs containing 111 prey items in the fall compared with 44 stomachs containing 920 prey items in the spring. In addition, 47% of stomachs were empty in the fall compared with only 1% in the spring. These differences have at least 2 possible explanations that could be related to differences in climate or sampling methods between seasons. In the Northern Redback Salamander, a species slightly smaller than the Del Norte Salamander, foraging behavior was strongly associated with rainfall, and food limitation was severe on hot, dry days (Jaeger 1980). These salamanders consumed large quantities of prey when moisture conditions were suitable (Jaeger 1980). In our study area the fall season is warm and dry in contrast with spring, which is cool and wet, and so we only sampled when weather conditions were appropriate for salamander surface activity. As a result, the duration of the fall sampling season was short relative to the spring season. Additionally, cool, wet spring conditions may increase forest productivity and thus increase invertebrate abundance. The longer duration of suitable conditions for surface activity and potentially higher invertebrate availability in spring likely offers more foraging opportunities than in fall. Del Norte Salamanders in our study area may respond to climatic differences between the seasons by foraging more actively and frequently in spring than in fall, which may correspond to an increased number of prey items in their diet in spring.

Alternately, seasonal differences in the numbers of prey items and other diet indices may be attributable to differences in sampling methods. In spring, we captured salamanders using time-constrained searches, which entail searching through talus, leaf litter, and wood debris to find salamanders in their refugia. In fall, we sampled salamanders using pitfall traps, a passive sampling method that requires salamanders to leave refugia and fall into the traps. While many invertebrates fall into pitfall traps, it is not known if salamanders forage while restrained in these traps. However, if they do, they would be most likely to encounter prey such as spiders and ants which tend to be active on the surface of the forest floor, rather than soil-associated species such as termites and oribatid mites or flying insects such as caddisflies. Additionally, if salamanders do not forage within traps, diet analysis would be biased toward a lower number of prey items of those species that have a short gut passage time. In a study of the Northern Redback Salamander, termites passed through the gut in an average of 4 d and ants in an average of approximately 6 d (Gabor and Jaeger 1995). Given that pitfall traps were checked every 5 d in our study, it is possible that the prevalence of some insects in the diet was underestimated due to gut passage times.

Adult Del Norte Salamanders did not appear to feed discriminately based on prey size. Adult salamanders consumed large and small prey. Subadults primarily fed on small prey items, which may be a result of gape limitation. Similarly in the Northern Redback Salamander, prey size was related to head size of juveniles

(Maglia 1996). In a comparative study of the feeding ecology of four northwestern plethodontids, Lynch (1985) found that Arboreal Salamanders (*Aneides lugubris*), which have large head widths compared to Speckled Black Salamanders (*A. flavipunctatus*) of equivalent body size, tend to take larger prey. He also found that the California Slender Salamander (*Batrachoseps attenuatus*), a species with small head width relative to Arboreal Salamanders of similar size, took smaller prey. In fall, larger prey items such as orthopterans and spiders had greater importance values for adult salamanders, whereas in spring, smaller prey items such as ants and springtails had greater importance values. This may be a result of seasonal differences in the size of available prey.

The one vertebrate prey item identified during this study was a juvenile Del Norte Salamander removed from the stomach of an adult Del Norte Salamander. This is the first case of cannibalism in this species. Cannibalism has been reported in the Northern Redback Salamander (Heatwole and Test 1961) and in Dunn's Salamander (Altig and Brodie 1971).

Our data indicate that no particular prey item dominates the Del Norte Salamander food base. However, because we did not determine prey availability, prey selection or avoidance could not be established. Prey items eaten by Del Norte Salamanders were similar to common prey consumed by other salamander species of Northern California and Oregon including the California Slender Salamander (Adams 1968; Bury and Martin 1973; Maiorana 1978), Clouded Salamander (*A. ferreus*; Storm and Aller 1947; Bury and Martin 1973; Whitaker and others 1986), Common Ensatina (*Ensatina eschscholtzii*; Zweifel 1949; Altig and Brodie 1971; Bury and Martin 1973), and Dunn's Salamander (Dumas 1956; Altig and Brodie 1971). In spring, adult Del Norte Salamanders consumed fewer prey items on average than subadults (9.9 vs. 20.9 per stomach), and adult salamanders did not appear to feed discriminately based on prey size. This is consistent with the conclusions of other plethodontid diet studies that these salamanders are opportunistic sit-and-wait predators (Lynch 1985; Petranka 1998).

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