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TERRITORIAL SALAMANDERS EVALUATE SIZE AND CHITINOUS CONTENT OF ARTHROPOD PREY

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Feeding territories provide an interesting area in which to study the behavioral mechanisms of food selection, because theories of territorial economics (Brown, 1964) and of foraging economics (Stephens and Krebs, 1986) become closely allied. Foraging decisions by the territorial defender may be influenced not only by changing densities of various prey types, but also by other environmental fluctuations, by intrusions from food competitors and predators, and by opportunities for courtship. Yet if defending a particular area is crucial to a territorial resident's future fitness, then the ability of the resident to move to another area for foraging is limited. The red-backed salamander (Plethodon cinereus) is a territorial species confronted with several conflicting demands on its foraging abilities.

Plethodon cinereus (family Plethodontidae, the lungless salamanders) is widely distributed in forests of eastern North America. It is strictly terrestrial, lacking any aquatic life-stage, and it can reach high densities (mean of 2-3 individuals per square meter) in the leaf litter or under rocks and logs on forest floors (Jaeger, 1979). Being amphibians and lungless, red-backed salamanders must maintain a moist skin, and so their foraging behavior is greatly affected by alternating periods of rainy and rainless weather. During and shortly following a rainfall, salamanders forage in the leaf litter and their stomachs are usually packed with prey (Jaeger, 1972, 1980). During rainless periods, though, the leaf litter dries and salamanders are forced into moist patches under rocks and logs (for individuals that have established feeding territories) or into fossorial crevices (for those that have not established such territories) (Jaeger, 1979; Mathis, to be published). Territorial individuals apparently are able to crop a small but renewable number of prey

during dry periods (Jaeger, 1980) under and around cover objects while those without territories, in underground refugia, essentially are restricted from foraging until the next rain (Fraser, 1976). Periodic rainfall, then, establishes a scenario whereby prey remain abundant in the leaf litter but vary temporally in availability to the salamanders. Territorial behavior, by males and females separately, appears to be primarily directed at protecting prey from competing salamanders, and it involves pheromonal advertisement (Jaeger, 1986; Jaeger et al., 1986; Home and Jaeger, 1988), visual agonistic displays (Jaeger, 1984; Home, 1988), biting of intruders (Jaeger, 1981), and consequent exclusion of intruders (Jaeger et al., 1982b).

In an attempt to elucidate the interaction of territorial defense and foraging tactics of red-backed salamanders, a number of experiments were performed in the laboratory. Briefly, these experiments revealed the following information. (1) Given two species of dipterans at varying densities, the salamanders elected an indiscriminate diet at low prey densities but specialized on the larger prey species at higher densities; specialization occurred by "ignoring" the smaller flies when they were encountered. The salamanders switched from pursuit to ambush tactics with increasing prey densities (Jaeger and Barnard, 1981). (2) Salamanders used encounter rates in assessing densities of the dipteran prey (Jaeger et al., 1982a). (3) Salamanders learned through foraging experience to assess profitabilities of the prey types (Jaeger and Rubin, 1982). (4) Salamanders sacrificed initial caloric yield until they had established marked (with pheromones) territories and then altered to a higher sustained caloric yield (Jaeger et al., 1981). (5) When salamanders in established territories were exposed to increasing threats of intrusion (by pheromones of conspecifics or by conspecifics themselves), the residents increasingly switched from a specialized diet (as above) at high prey densities to an indiscriminate diet at the same prey densities. Time subtracted from foraging was added to time devoted to territorial defense (Jaeger et al., 1983).

Red-backed salamanders feed on a broad variety of invertebrates inhabiting the detritus of forest floors (Jaeger, 1972).

Consequently, their diets include termites (Isoptera) and spring-tails (Collembola), which are lightly armored with chitinous exoskeletons, and ants (Hymenoptera: Formicidae) and beetles (Coleoptera), which are heavily armored with exoskeleton. Digesting the chitin of ingested prey is difficult for many predators, and so the amount of chitin encasing a prey item may strongly influence the profitability of that item from the viewpoint of the predator. For Plethodon cinereus, the chitinous content of a prey item apparently does not affect the salamander's assimilation efficiency (A.E.) for that item; Bobka et al. (1981) reported that both chitinous ants and less chitinous dipterans (Drosophila) were assimilated equally at a given temperature (about 80% A.E. for both prey at 20 C rising to 90% A.E. for both at 10 C). However, Jaeger and Barnard (1981) noted that passage time through the digestive tract of *P. cinereus* is much faster for the dipterans (approximately 70 h) than for the ants (approximately 112 h) at 15 C. Passage time logically determines the rate at which new prey can be ingested. For red-backed salamanders, which obtain most of their prey during often short periods of rainfall, maximizing ingestion rate (and passage time) during those periods may be critically important in maximizing net energy yield from foraging.

The above concepts led to a hypothesis by Jaeger and Barnard (1981) concerning diet selection by *P. cinereus*. When prey are abundantly available, during rainfalls, salamanders should specialize, thus minimizing chitin in their diets. (1) If two prey items differ only in size (such as two species of flies), salamanders should choose the larger one because of its greater gross energy content and relatively less chitin (from surface to volume ratios). (2) For prey types differing in armor (such as termites and ants) but equal in size, the less armored one should be chosen. (3) Given a choice of a larger, heavily armored prey and a smaller prey with reduced chitin, the salamander should choose the prey type with the higher net energy profit per unit of digestion time. These three points assume equal assimilation efficiencies and energy expended per ingested prey. During times when prey are low in availability, such as rainless periods,

salamanders should be less selective, and heavily armored prey should increase proportionally in the diet. The goal of the research reported here was to provide a first test of Jaeger and Barnard's (1981) hypothesis, utilizing P. cinereus in a natural forest habitat.

DIET DIVERSITY

In order to identify the major and minor taxa of invertebrates found in the diet of Plethodon cinereus, I utilized data previously collected in 1970 for other research purposes (Jaeger, 1980). Quadrates 15 x 100 m were established on the forest floor of Black Rock Mountain, Shenandoah National Park, Virginia. Fifteen quadrates were randomly sampled, one on each of 15 consecutive days from 25 July through 8 August, but no quadrate was sampled more than once. In each sample, 30-35 adult red-backed salamanders were collected, were immediately killed by anesthesia, and were preserved (including stomachs) in 10% formalin. The contents of their stomachs were later removed, and the prey contained therein were identified to taxa and were measured to determine the volume of each prey item (Table 1). More details concerning collecting and preserving the salamanders and processing the ingested prey were given in Jaeger (1980).

Table 1 shows that red-backed salamanders have a large diversity of prey types in their diet. The insects were even more impressive in diversity when partitioned by families: COLEOPTERA (Anobiidae, Cantharidae, Carabidae, Chrysomelidae, Cicindelidae, Coccinellidae, Cucujidae, Curculionidae, Elatidae, Nitidulidae, Scarabaeidae, Staphylinidae, Tenebrionidae); COLLEMBOLA (Entomobryidae, Sminthuridae); HEMIPTERA (Miridae, Nabidae); HOMOPTERA (Aphididae, Cicadellidae, Delphacidae, Membracidae); HYMENOPTERA (Braconidae, Ceraphronidae, Cynipidae, Eucharitidae, Eulophidae, Figitidae, Formicidae, Ichneumonidae, Mymaridae, Platygasteridae, Pompilidae, Pteromalidae, Scelionidae, Trichogrammatidae); ISOPTERA (Rhinotermitidae); LEPIDOPTERA (larvae not identified to taxa); ORTHOPTERA (Blattidae, Gryllidae); PSOCOPTERA (Eupsocidae). The DIPTERA (Brachycera, Cyclorrhapha, Nematocera) could not be identified to family level.

Table 1.—Percentages (by number and volume) of invertebrate taxa found in the stomachs of 519 salamanders collected over 15 consecutive days. Total number of prey identified was 4752.

<u>TAXA</u>	<u>% BY NUMBER</u>	<u>% BY VOLUME</u>
Nematoda	0.02	0.002
Gastropoda	2.02	6.048
Oligochaeta	0.34	17.652
Acarina	50.02	9.126
Araneae	2.67	7.482
Isopoda	0.02	0.005
Chilopoda	0.97	8.451
Diplopoda	0.34	1.260
Insecta		
Coleoptera	2.36	19.452
Collembola	13.09	3.428
Diptera	20.85	7.474
Hemiptera	0.21	1.298
Homoptera	0.35	2.011
Hymenoptera	5.49	9.425
Isoptera	0.15	0.085
Lepidoptera (larvae)	0.04	5.402
Orthoptera	0.08	0.863
Psocoptera	0.80	0.536

The data in Table 1 demonstrate that some prey (such as Acarina) comprise a large proportion of the diet by number but not by volume, while other prey (such as Coleoptera) comprise a large proportion of the diet by volume but not by number. The data in Table 1 will later be used to formulate analyses of experimental results concerning choice of diet by red-backed salamanders.

DIET SELECTION

The experimental test of Jaeger and Barnard's (1981) hypothesis of diet selection was performed during 1982 in the southern Blue Ridge Mountains of Virginia. I compared the size distribution of prey ingested by salamanders and of prey available in the environment under conditions of both wet and dry forest litter.

Methods

Two 15 x 100 m quadrates were established on the forest floor adjacent to each other. On 26 July, 12 h of heavy rain fell, and I randomly chose one quadrate for study. Forty Tanglefoot traps were placed on the forest floor (in randomly selected positions within the quadrate), where red-backed salamanders were known to forage during wet periods (Jaeger, 1972, 1979). Each trap consisted of a 15 cm diameter circle of filter paper coated with Tanglefoot spray, a sticky material commercially developed for entrapping invertebrates. Each trap was placed on the leaf litter with an inverted petri dish serving as an "umbrella", and litter was placed over the dish. Twenty-four hours later, 31 traps were recovered (nine had been destroyed) and were stored separately in 70% ethanol. Thirty-one red-backed salamanders were then collected from the litter, each salamander being at 0.5-2.0 m distance from a trap (n = 31 salamanders and 31 traps). Salamanders were killed immediately and were preserved as in the 1970 analysis (see above). Because red-backed salamanders require about 24 h to pass prey through their stomachs at 17 C (mean soil temperature upon capture), both stomach contents and contents of the traps should reflect 24 h of salamander foraging and "trap foraging".

No rain fell from 27 July until 2 August. On 31 July, the leaf litter appeared to be dry, so 40 additional Tanglefoot traps were placed in the second quadrate. These traps were positioned next to randomly selected rocks; because red-backed salamanders apparently forage under and near cover objects (which act as patches of moisture) during dry periods (Jaeger, 1972, 1979), these traps were intended to sample prey available to salamanders confined to a small distance around their cover objects. After 24 h, 30 traps were recovered (10 had been destroyed) and preserved (as above), and 30 salamanders were collected from under rocks within 0.5-2.0 m of the traps and were immediately killed and preserved (n = 30 salamanders and 30 traps). Thus, the sampling protocol for both wet and dry days was the same (0.5-2.0 m between traps and salamanders).

To determine whether my visual estimates of "wet" and "dry"

days were correct, I used a Soilmoisture Probe model 2900 (tensiometer) to record ambient moisture at 40 randomly selected positions within each quadrat while salamanders were being collected. Each preserved salamander was measured for snout-vent length (SVL) and head width, and its stomach was removed and opened. The length and mid-body width of each intact prey item was measured using a dissecting scope fitted with an ocular micrometer, and the volume of each item was estimated by converting to the volume of a cylinder or a sphere, as appropriate. Prey items removed from traps were measured similarly. The number of salamanders collected each day was deemed sufficient for analysis of stomach contents, because Fraser (1976) showed that approximately 21 stomachs of Plethodon cinereus were necessary to estimate prey volume diversity. Trapped prey that were too wide to be ingested by salamanders (i.e., greater than the salamanders' head widths) were deleted from the samples, as were trapped prey that were smaller than the smallest item ingested by any salamander.

These data allowed me to compare the volume-distribution and taxa of prey ingested under two conditions of mobility by salamanders (wet versus dry days) with the volume-distribution and taxa of prey available to salamanders in the leaf litter.

Sizes of Prey

As anticipated, the forest floor was significantly wetter on the rainy sampling day than on the rainless sampling day (Table 2). The salamanders collected on the dry and wet days did not differ significantly either in snout-vent length or in head width (Table 2); this indicates that individuals from the two sampling days were capable of eating the same total volumes and individual sizes of prey.

Salamanders on the dry day had significantly fewer prey per stomach than those on the wet day and significantly less total volume of prey per stomach (Table 2). Therefore, as found in an earlier study (Jaeger, 1972), the dry-day salamanders had less success at foraging than did the wet-day conspecifics. The number of prey "captured" by the traps was significantly less on the dry day (218/30 traps, $\bar{x} = 7.3/\text{trap}$) than on the wet day (450/31

Table 2.—Means (and sample sizes) for soil moisture, snout-vent length (SVL), and head width of salamanders, number and total volume of prey ingested, and volume of individual prey items found on traps and in stomachs for dry and wet days.

TAXA	$\bar{X}$ /DAY			n/DAY		P	
	DRY	WET		DRY	WET		
Soil moisture	18	0	cb	40	40	0.0002	*
SVL	31	32	mm	30	31	0.243	
Head width	4.1	4.0	mm	30	31	0.372	
No. prey/stomach	1.5	16.8	Prey	30	31	0.0002	*
Total vol. prey/ stomach	8.1	44.1	mm ⁵	30	31	0.0002	*
Vol. each potential prey (on traps)	1.8	1.5	mm ³	218	450	0.941	**
Vol. each prey (in stomachs)	5.3	2.6	mm ³	46	522	0.0008	*

* Significant difference, Mann-Whitney U test, two-sided, alpha = 0.05. ** Variances were homoscedastic between days.

traps, $\bar{x}$ = 14.5/trap): Mann-Whitney U test, P = 0.002 two-sided.

The distribution of volumes of potential prey items found on the traps did not differ significantly between the 218 dry-day invertebrates and the 450 wet-day invertebrates (Table 2); thus, the sizes of potential prey available to salamanders on dry and wet days apparently were the same. However, the mean volume of each prey item found in the stomachs of salamanders was significantly greater on the dry day than on the wet day (Table 2); therefore, wet-day salamanders ingested, on average, smaller prey items than did dry-day salamanders.

In summary, salamanders ingested more prey, greater total volumes of prey, but smaller individual prey items, during wet-day foraging than during dry-day foraging.

Because the volume-distributions of potential prey on traps were not statistically different between the two days (Table 2), the prey volumes from traps are pooled into a single set in Fig. 1 for ease of visual inspection. However, Table 3 utilizes the dry-day and wet-day traps separately for statistical comparisons between stomachs and traps on those two days.

The dry-day salamanders ingested significantly larger prey items than those found on the dry-day traps (Fig. 1, Table 3), indicating that "hungry" salamanders did specialize on larger

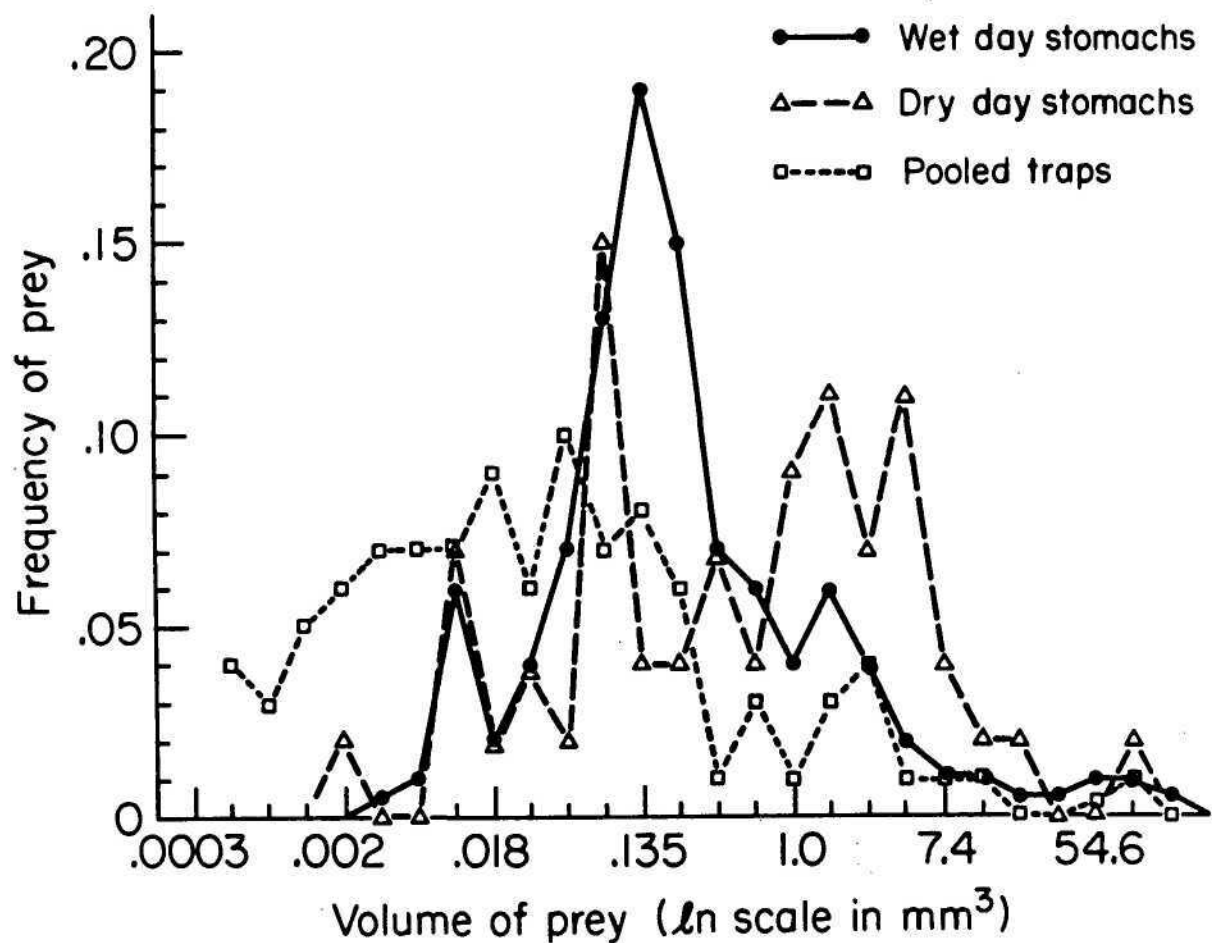


Figure 1.—Frequency of prey as a function of size-class (volume) of prey from (a) stomachs of salamanders collected on a "wet" day (superior foraging time), (b) stomachs of salamanders collected on a "dry" day (poor foraging time), and (c) traps pooled for the two days.

prey, rather than resorting to a strictly generalist diet. This occurred because the salamanders virtually excluded from their diet prey less than 0.002 mm³ while concentrating on prey of two volumes: 0.08 mm³ and from 1.0–4.5 mm³ (Fig. 1).

The wet-day salamanders also ingested significantly larger prey than those found on the traps (Fig. 1, Table 3). These salamanders failed to ingest prey of less than 0.004 mm³ and were essentially unimodal in choice of prey-volume (0.135 mm³), biased toward the larger of the most abundant prey-volumes on the traps (Fig. 1).

Therefore, both dry- and wet-day salamanders took proper-

Table 3.—Comparisons of volumes of ingested prey and trapped potential prey on dry and wet sampling days; n = number of prey in the sample.

<u>DAY</u>	<u>x VOL. (mm³) EACH ITEM INGESTED</u>	<u>n</u>	<u>x VOL. (mm³) EACH ITEM ON TRAPS</u>	<u>n</u>	<u>P</u>
Dry	5.3	46	1.8	218	0.0001 *
Wet	2.6	522	1.5	450	0.002 *

* Significant difference, Mann-Whitney U test, two-sided, alpha = 0.05.

tionally larger prey than were available in the forest litter (Table 3), but the wet-day salamanders chose prey of smaller size than their dry-day conspecifics (Table 2).

Taxa of Prey

So far, I have demonstrated that red-backed salamanders shifted from ingesting smaller prey items on a superior foraging wet day to larger prey items during a poor foraging dry day. Jaeger and Barnard's (1981) hypothesis would predict that this change in diet represented a shift in prey taxa eaten: from smaller, lightly armored prey on the wet day to larger, heavily armored prey items on the dry day. I now test this hypothesis with taxonomic data from those two days.

Based on the large sample of stomach contents in Table 1, I chose four taxa for comparisons between the wet and dry days: Coleoptera and Hymenoptera (both with relatively hard exoskeletons and relatively large in volume per individual) and Collembola and Diptera (both with relatively soft exoskeletons and relatively small in volume per individual). A discussion of arthropod cuticle and chitin may be found in Miller (1980). Individuals of the four taxa combined from wet- and dry-day traps were of the following sizes (volumes): Coleoptera — range = 0.95-92.4? mm³ (x = 17.92 mm³); Hymenoptera — range = 0.08-69.91 mm³ (x = 3.75 mm³); Collembola — range = 0.04-1.81 mm³ (x = 0.43 mm³); Diptera — range = 0.13-12.57 mm³ (x = 2.06 mm³).

I computed the percentages (by volume) of Coleoptera, Hymenoptera, Collembola, and Diptera found in the stomachs and on the

Table 4.—The percentages (of volumes) of four taxa of insects found in the stomachs of salamanders and on the traps from the wet day and the dry day. Although only four taxa of prey are included here, the percentages are based on all taxa found in the samples.

<u>TAXA</u>	WET DAY		DRY DAY	
	% PREY IN: <u>STOMACHS</u>	<u>TRAPS</u>	% PREY IN: <u>STOMACHS</u>	<u>TRAPS</u>
Coleoptera	2.9	18.9	8.5	12.1
Hymenoptera	1.5	13.3	10.0	11.7
Collembola	7.5	7.1	3.9	4.1
Diptera	9.9	8.1	3.3	2.7
All other	78.2	52.6	71.3	69.4

traps during the wet day and the dry day. Statistical comparisons of the results were not performed because of the small number of prey ($n = 46$) found in the stomachs ($n = 30$) on the dry day. However, Table 4 provides information for useful inferences.

On the dry day when salamander foraging was relatively poor, the stomachs and traps had similar proportions of the various taxa (Table 4). Thus, the salamanders apparently foraged indiscriminately among these four taxa of prey.

On the wet day when foraging was superior, far less proportional volumes of Coleoptera and Hymenoptera showed up in the stomachs of salamanders than were on the traps (Table 4). However, Collembola and Diptera were approximately proportionally equal for stomachs and traps on that day.

DISCUSSION

Food Selection and Territoriality

These data support the hypothesis that red-backed salamanders tend to eliminate prey items with hard exoskeletons from their diets during superior (wet) foraging periods, even though those prey items may be among the largest (in body size) available to the salamanders. The data cannot, of course, determine whether such a shift in diet maximizes net energy (or nutritional) yield for the salamanders. A more highly controlled experiment is required to do that, where the behavior of a for-

aging salamander can be closely observed and its energetic costs and benefits during foraging can be derived. Such experiments are extremely difficult to perform in natural leaf litter habitats and so must be confined to the laboratory, as in Jaeger and Barnard (1981). Still, red-backed salamanders do employ mechanisms of food selection that are likely related to the amount of time necessary to pass food items through the digestive tract.

The rate of food passage is important to these salamanders because of the constraint of "pulse feeding". When the leaf litter on the forest floor is wet, red-backed salamanders move into it for foraging, but this opportunity may last for only a few days following a rain, depending on evaporation (which in turn is related to ambient temperature, relative humidity, and wind speed). Thus, salamanders are confronted with rich foraging periods that may be separated by variable periods of poor foraging, when territorial individuals are confined to the vicinity of cover objects and nonterritorial individuals apparently cease foraging underground. During a rich foraging period, a salamander that eats lightly armored prey, such as dipterans, can pass a greater volume of prey through its digestive tract in a given period of time than an individual that eats heavily armored prey, such as ants, although equal volumes of flies and ants yield the same energetic benefits to the salamander (Bobka et al., 1981). Thus, salamanders seem to avoid having hymenopterans and coleopterans clogging the digestive tract when softer prey are readily available. During drier times when prey are scarcely available, any type of prey item seems to suffice, and armored prey are ingested.

One intriguing problem is how salamanders differentiate among taxa of potential prey that vary in thickness (and chitin content) of their exoskeletons. Salamanders may use some innate recognition template (visual or olfactory), being genetically programmed to differentiate between, say, coleopterans and collembolans. Although Plethodon cinereus ingests a broad diversity of prey types (Table 1), it is possible that individuals employ some general guidelines to differentiate among major groups. If so, olfactory cues are likely to be important, because Roth (198?)

reported that "visual prey schemata can be rather simple" for salamanders. Indeed, *P. cinereus* can locate prey purely on the basis of olfactory cues (David and Jaeger, 1981), although visual cues are also important (Jaeger et al., 1982a; Roth, 1987).

Jaeger and Rubin (1982) showed that red-backed salamanders can learn to judge the profitabilities of dipteran prey through foraging experience, and several experiments have documented the importance of early learning and a "sensitive period" during the ontogeny of feeding behavior (see review in Roth, 1987). However, a more finely tuned understanding of the behavioral mechanisms of food selection by terrestrial salamanders must await more research on sensory modes utilized by salamanders in choosing prey from the vast diversity in the environment.

Although knowledge of the territorial behavior of red-backed salamanders is still fragmentary, general concepts are presently falling into place. Males and females establish separate territories under, and perhaps around, rocks and logs on the forest floor, but many smaller sized (presumably younger) individuals lack territories (Mathis, to be published). During dry periods, salamanders with territories feed indiscriminately (by taxa) on the scanty prey therein, although indiscriminate foraging may not be true in particularly rich territories, such as under logs containing soft bodied termites. When rain or fog occurs, salamanders move into the leaf litter and have more flexibility in seeking rich patches of prey, such as earthworms, dipteran larvae, spiders, springtails, termites, and lepidopteran larvae. Yet territorial individuals are probably prevented from wandering far from their territories because of the risk of territorial takeovers from nonterritorial "floaters" (Nunes and Jaeger, 1989). Thus, terrestrial, forest floor salamanders are ultimately constrained in foraging mobility by the risk of desiccation and may be proximally constrained, even during the best of foraging times, by the need for territorial defense. However, red-backed salamanders reap a large reward from their fluctuating environment; population biomass of *P. cinereus* in a forest can exceed that of all species of birds combined during peak avian density of the breeding season (Burton and Likens, 1975). The low metabolic costs,

high assimilation efficiency, and foraging skills of the salamanders contribute to their high densities and wide distribution in eastern North America.

Food Selection and Mate Selection

Fecal material is a consequence of foraging, and females of Plethodon cinereus seem to take an inordinate interest in fecal pellets of males during the courtship season. Walls et al. (1989) found, in a laboratory experiment, that females used their snouts (where chemosensory structures occur) to "squash" male fecal pellets. Females then chose to reside near pellets that were a residue of a high quality diet (soft exoskeleton termites) compared to pellets from a low quality diet (hard exoskeleton ants). Walls et al. (1989) also found that in a natural forest habitat, males that had fed on termites had proportionally greater access to gravid females than did males that had fed on ants. Apparently females make some estimate of male quality per se or of male territorial quality in a simple way: by assaying male fecal material. These results suggest that a male's choice of diet may affect his fitness not only indirectly through his own health, but also directly through mate choice by females.

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