

AN ABSTRACT OF THE THESIS OF

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Title: THE BEHAVIORAL ECOLOGY OF LARVAL AND NEOTENIC  
NORTHWESTERN SALAMANDERS (AMBYSTOMA GRACILE)

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In the summers of 1973, 1974 and 1975, I investigated population age structure and density, and behaviors relating to habitat selection, predator avoidance and intraspecific interaction in a population of northwestern salamanders in a lake in the Oregon Cascade Mountains. The study was carried out by skin- and scuba-diving at night, observing or netting the salamanders directly.

Population density and age structure remained stationary from 1973 to mid-1975, when density fell and the age structure shifted toward domination by older age classes. This change in the population was apparently due to the stocking of more fish into the lake.

The salamanders had definite depth preferences, with slight but significant differences in preference between age classes. No salamander was found in water deeper than 1.3 m. The salamanders utilized bare mud substrate much less than would be expected on the basis of frequency of occurrence of the substrate, and utilized

substrate covered with twigs and wood chips more often than would be expected. When escaping from a simulated predator attack the salamanders avoided bare mud completely. Those animals occupying areas covered with thick grass (Isoetes) tended to move to areas with much sparser grass clumps, when escaping. Preferences based on temperature, oxygen tension or the presence of large pieces of cover such as logs were not evident.

Frequencies of predator avoidance behaviors were different in the different age classes. In the case of one-year olds, behavioral frequencies changed after the stocking of new fish. Before the stocking, the one-year olds tended to avoid orienting in a direction perpendicular to the shore/deep water axis (laterally). If they did orient in this direction, they turned away from it when escaping a simulated predator attack. After the stocking, orientation and direction of escape were essentially random. At the end of the escape movement those one-year olds oriented towards shore and/or in deeper water (>70 cm) burrowed into the substrate; those oriented towards deep water and/or in shallow water (<70 cm) remained on top of the substrate.

Two-year olds were essentially random in orientation and direction of escape. At the end of the escape movement those individuals in deeper water burrowed into the substrate; those in shallow water remained on top of the substrate.

Three-year old and older salamanders demonstrated quite complex predator avoidance behavior. Animals in this age group tended to avoid orienting laterally, turning towards deep water much more often than would be expected on a random basis. Those animals in deeper water oriented toward deep water; those in shallow water oriented toward shore. These individuals moved straight ahead when escaping a simulated predator. Laterally-oriented animals avoided escaping straight ahead: those in deep water turned towards deep water, while those in shallow water turned towards shore. Most (75%) of the three-year-olds burrowed into the substrate at the end of the escape movement.

The salamander population was aggregated. This aggregation may have involved some components of habitat selection, but was not produced by a thinning-out of animals as depth increased.

Analysis of individual and nearest neighbor ages revealed that young (small) salamanders avoided associating with older (larger) animals. This avoidance behavior began to disappear in the middle of the second year of life, as the one-year olds approached the two-year olds in size.

The observed behaviors appeared to be chiefly responses to predation by introduced trout. They apparently constitute the principal mechanism permitting the salamander population to persist under a regime of predation. The behaviors are probably learned; the variation in behavior between age classes was probably due to variation in predation pressure produced by fluctuations in stocking success of the fish.

The Behavioral Ecology of Larval and Neotenic Northwestern  
Salamanders (Ambystoma gracile)

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James Thomas Taylor

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THE BEHAVIORAL ECOLOGY OF LARVAL AND  
NEOTENIC NORTHWESTERN SALAMANDERS  
(AMBYSTOMA GRACILE)

INTRODUCTION

Predation is one of the most common behaviors in the animal world. Predation is also one of the most widely discussed community processes in biology. Yet ecologists have little concrete idea of the mechanisms which permit predator-prey associations to persist through time, or of the role of predator-prey interactions in determining community stability.

This problem is manifold. Part of the problem stems from a difficulty with semantics. Theoreticians have given us some elegant mathematical definitions of stability and persistence, which are sometimes not easily interpreted in biological terms (cf. Botkin and Sobel, 1975). For the purposes of this study I will define persistence in a predator-prey system as the continuance of the system through time without extinction of any population in the system. Since persistence is a component of stability, I will also postulate that instability in a system leads to lack of persistence. While avoiding the issues of rigorous definitions, these conventions are biologically operational and consistent with formal definitions.

Theoreticians have also built a number of models of predator-prey interactions, but these models rise and fall on their assumptions.

and often give equivocal or contradictory results. For example, MacArthur (1955) constructed a formal proof to demonstrate that community stability increases with the addition of predator-prey interactions. May (1973) demonstrated the converse: complex food webs are basically unstable, and should collapse into simpler systems with a loss of persistence.

Laboratory workers have fared no better. Controlled experiments set up to mimic predator-prey interactions (e. g. , Gause, 1934; Huffaker, 1958; Maly, 1969; Luckingbill, 1974) never persist for more than a few generations without the addition of some unnatural complexity such as an atmospheric thickener (Luckingbill, 1973).

Another approach involves the attempt to fit real data to the predictions of various mathematical models, but here too there are difficulties. First of all, there is a dearth of quantitative information on natural predator-prey populations. Second, goodness of fit between a model and real data is not a test of the model and its assumptions. Third, real data may fit more than one model. For example, the well known lynx-hare cycles of boreal Canada (MacLulich, 1937) have been interpreted as a neutrally stable Lotka-Volterra system (although Leigh (1968) has found a relatively poor fit to this model); as an equilibrium system disturbed by random environmental noise (Moran, 1953); as a stable limit cycle (May, 1973); or, facetiously, as the consequence of hares eating lynx (Gilpin, 1973).

A final difficulty with general analysis of predator-prey systems arises from the observation that different circumstances require different theories. For example, Paine (1966) found that predation maintained species diversity in an intertidal community, allowing the community to persist. However, Addicott (1974) observed the opposite in an aquatic community inside Pitcher Plants. Obviously, neither situation produces analytic description of the other. Along this line, we may also observe that introduction of an exotic predator sometimes drives a prey species to extinction (e.g., several Caribbean solenodons [Mammalia, Insectivora] have been exterminated by introduced mongooses [IUCC, 1972]), and sometimes such an introduction has little apparent effect. Even such highly studied groups as the predator or parasitoid systems used in biological control of arthropod pests do not admit to totally predictive results.

The best studies on predator-prey systems have been done by workers in biological control programs (e.g., Holling, 1961; Huffaker, 1958; Watt, 1959). This work has often involved a combination of laboratory experiments with quantitative field studies and modeling techniques. However such studies have concentrated mainly on predator tactics; little consideration has been given to prey responses.

The solution of these difficulties can only lie in more detailed description of various predator-prey systems. While such procedure may never produce a predictive body of knowledge, it can elucidate some of the mechanisms of community persistence and lead to conciliation between theory and the real world. Description can also increase our knowledge of prey tactics, which has lagged far behind consideration of predation from the predator's point of view.

There are several requirements for real world study of predator-prey systems. The populations of interest must be well defined, and preferably relatively small. Small islands usually harbor such populations, as do small ponds or lakes: the land-water interface effectively delineates the populations, and small areas or volumes are tractable to efficient study. Ideally, the system should be quite simple in species composition, perhaps two or three species, to preclude confusing interactive effects not involving predation. Also, the animals in the system should be relatively large or otherwise easily observable. While good work has been done with microscopic organisms (e. g. , Brooks and Dodson, 1965), the level of resolution is rather low and enumeration techniques are quite tedious.

There is also a problem with extracting meaningful information from non-experimental descriptions. Although a descriptive study may implicate certain processes or mechanisms as operating in a system, it cannot prove their existence or disprove the operation of

alternatives. In order to draw a conclusion from a description, then, the observer must be able to refute alternate conclusions with logic, intuition, or the auxiliary observations that always occur to a good natural historian. If such refutations are possible, descriptive observation can be a powerful scientific approach, though certainly not as powerful as the hypothetico-deductive method.

With these considerations in mind, I undertook a study of a simple predator-prey system composed of an introduced vertebrate predator, and a vertebrate prey species which had formerly been a top carnivore in its community. This system comprised larvae and paedogenetic adults of the northwestern salamander (Ambystoma gracile) preyed upon by introduced cutthroat and brook trout (Salmo clarki and Salvelinus fontinalis) in a lake in the Oregon Cascade Mountains. The only other resident vertebrate in the lake was the rough-skinned newt, Taricha granulosa, a salamander which is not preyed upon by fish (Efford and Mathias, 1969). The salamanders are native to the area; the trout were introduced no earlier than 1920, and possibly as late as 1950 (Jim Griggs, personal communication). The northwestern salamanders have thus coexisted with their predators for at least 25 years without the benefit of a coevolved relationship. Accepting this coexistence as proof of persistence of the system, I set out to determine the mechanisms by which the salamanders have avoided predation to the point of extinction.

After some preliminary observations on population structure, I formed the hypothesis that at least some of the salamanders were avoiding predation with specific behaviors. I then devised a protocol for quantification of several types of behavior which could conceivably be related to predator avoidance. These observable behaviors included: (1) habitat selection, (2) orientation and escape responses, and (3) dispersion and intraspecific interaction.

The focus of the study thus became the quantification and description of salamander behavior.

## THE STUDY AREAS

The bulk of my studies was done at Fay Lake in Linn County, Oregon (T12S, R7E, Section 21). It is located within the Willamette National Forest, at a benchmark elevation of 1166 m. The lake covers 2.8 to 3.5 ha, depending upon the season, with a maximum depth of 4 m at spring high water. Much of the lake is less than 1 m deep (Figure 1). The soft mud bottom is composed of only 4% solid matter by volume, and supports only sparse vegetation. There are a few lily pads (Nymphaea) and liverworts (Ricciocarpus), and a mat of the alga Chara at the east end. The grass Isoetes grows in the shallows, spreading rapidly as the summer progresses. There are small stands of the sedge Carex in the shallows. The lake is surrounded by a hedge of Douglas spirea (Spirea douglassi), the lower branches of which are submerged during high water. The water level drops rapidly over the summer, however, as much as 1.4 m between mid-June and mid-September.

The State of Oregon stocks the lake with trout every two years. The fish are dropped as fingerlings from a height of 50 m by a "dive-bombing" airplane. The stocking of 1973 was a total failure, probably due to high water temperatures. The stocking of 1975 was a success. The trout cannot breed in the lake; there is no gravel in the lake for egg deposition (Lagler, Bardach and Miller, 1961), nor is there an

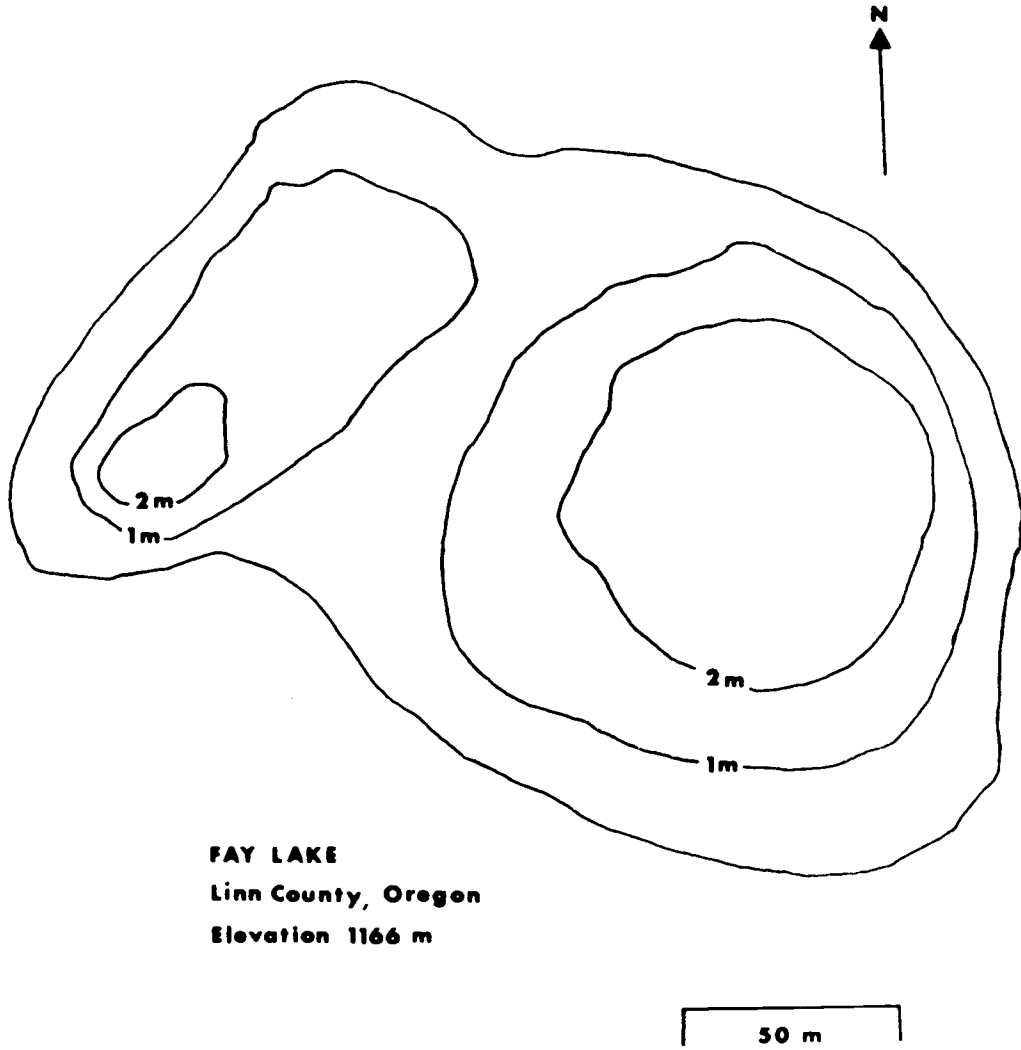


Figure 1. Map of the principal study area.



inlet or outlet stream. The lake is filled by precipitation, most of which falls as snow (up to 18 m a year).

Much of my work was done on two 30 x 50 m quadrats. Quadrat one was set up in the northwest corner of the lake (point A in Figure 1). Quadrat two ran at almost right angles to quadrat one, along the west shore (point B in Figure 1). Quadrat one was structurally homogeneous, with the bottom sloping gently to the south and little vegetation other than Isoetes and a few Carex. Quadrat two was structurally more heterogeneous. The bottom sloped to the east with a pitch of up to 20%. There were many submerged logs in the quadrat, and every type of substrate or vegetation in the lake occurred there, except for Chara and Nymphaea.

Fay Lake is frozen over from November to May or June, and snow bound even longer. In early spring, and late fall, I made auxiliary observations at Lost Lake, 10 km to the southeast, which is always accessible. This lake is much larger (ca. 25 ha), but is otherwise similar to Fay Lake.

For comparative purposes I also worked at Scott Lake, 24 km to the south and 300 m higher. This was a deeper lake with a maximum depth of 7.5 m at spring high water.

## THE NORTHWESTERN SALAMANDER

The northwestern salamander occurs from northern California to southern Alaska (Snyder, 1963), and from the Pacific Ocean east to the eastern slope of the Cascade Mountains. As in several other species in the family ambystomatidae, many individuals are paedogenetic, becoming sexually mature without metamorphosing from the larval stage. Such sexually mature larvae are also called neotenes, in reference to the retention of juvenile characteristics in an adult. In this paper, neotenic and paedogenetic will be used interchangeably.

Most high elevation populations of A. gracile, such as those in the Cascades, are putatively totally neotenic (Snyder, 1956). The typical neotene is from 12 to 15 cm in length, weighing from 10 to 25 g. They are mottled green or brown dorsally, with a venter ranging from white to all black. Yellow lateral spots may or may not be present. The high tail fin reaching to the back of the head, and the long plumose external gills are characteristic of a pond type larva (Noble, 1931).

Egg laying in the Cascade lakes takes place after the spring thaw has commenced, in May or June. Larvae hatch at a snout to vent length (SVL) of 6 to 9 mm. Metamorphosis, if it is to occur in an individual, usually takes place at a SVL of about 45 mm (Licht, 1975). Sexual maturity occurs after the individual exceeds 50 mm SVL (Efford and Mathias, 1969).

## METHODS

Ambystoma gracile in Fay Lake are aquatic and nocturnal, but can be approached quite closely by the careful swimmer. I therefore studied them by skin- and scuba-diving at night in various sections of the lake, using a 6 v diving light for illumination.

In summer of 1973 I collected approximately 65% of the animals seen, using a crinoline bag net (20 x 12 cm x 1 m deep) into which the salamanders could be driven with a push with the flashlight. After catching an animal I would gently push it to the bottom of the net bag, and confine it with a clothes pin snapped around the bag. I could thus capture and hold a number of salamanders without immediately transferring them to another container.

The next day I anesthetized the animals in 0.1% tricaine methanesulphate (Fiquel, Ayerst), measured head width and snout-to-vent length (SVL), and marked those animals greater than 40 mm SVL to indicate the area of the lake in which they had been captured. Marking was done by heat branding, or by sewing a colored thread to the dorsal fin. The salamanders were then agitated in cool, fresh water until they regained motility, at which time they were returned to the area from which they had been taken.

After watching and measuring a number of salamanders, I became convinced that I could distinguish four distinct size classes.

Graphing the frequency distribution of the measured SVLs produced a trimodal distribution skewed toward the larger sizes. This distribution coincided with those published by Efford and Mathias (1969) and Neish (1971); and with that from a population of neotenes in Owl Creek, Linn County, Oregon, which I studied during the winter. These four noticeable size classes changed a little with time, as the salamanders grew, but were roughly composed of salamanders of <25 mm SVL; between 30 and 45 mm SVL; between 50 and 55 mm SVL; and >55 or 60 mm SVL. To check my ability to visually categorize the animals underwater, I began to note the number of animals in each size class in the total collected nightly. The next day my observed size classifications were confirmed with calipers. I remain convinced that I can correctly categorize larval and neotenic A. gracile while underwater with an accuracy exceeding 95%. Of course there were a few animals which fell into the "in between" areas. Keying on allometry of the head with regard to body size, I believe that I can correctly size these animals too.

The four size classes correspond to the age classes of young of the year (<25 mm SVL); one-year olds (30-45 mm SVL); two-year olds (50-55 mm SVL); and three-years old or older (>60 mm SVL). This correspondence is confirmed by the growth studies of Snyder (1956), Efford and Mathias (1969); Neish (1971), Licht (1975), and by

my own observations on salamanders hatched and maintained in the laboratory.

In 1973, I also attempted to measure dispersion of the animals. While swimming a transect along the edge of one of the quadrats, I marked the position of each salamander seen by pushing a thin wand into the substrate. The next day I measured the distance between each pair of adjacent wands.

During the entire study I monitored temperature and oxygen tension at the top and bottom of the water column, and 10 cm underneath the substrate, using a YSI model 51 oxygen and temperature probe.

In 1974 and 1975 I confined my observations principally to two 30 x 50 m quadrats, using a refined observational protocol. For each animal seen in a quadrat I recorded the age, orientation of the head, substrate beneath the animal, and kind and direction of any object within 20 cm of the salamander. I then elicited an escape response, noting the direction and route of escape, the position and substrate chosen after escape, and the number of a flag inserted into the substrate at the point formerly occupied by the animal. The next day I measured the depth and distance to the nearest neighbor, at each marked point. These observations, the alternatives or units of measure involved, and the focus of each observation are summarized in Table 1. Analysis of individual sequence numbers, the number of

Table 1. Observational variables used to quantify salamander behavior, with alternatives or unit of measure, and type of behavior quantified by each variable.

Variable	Alternatives or Unit of Measure	Subject of Investigation
Date		
Transect		
Individual sequence number	1 to N	Intraspecific interaction
Age	1, 2, or 3	All
Age of nearest neighbor*		Intraspecific interaction
Orientation of head	Towards shore	Predator defense
Direction of escape	Laterally	Predator defense
	Toward deep water	
Shift in direction with escape*	0, 90°, 180°, 270°	Predator defense
Escape movement	Along substrate	Predator defense
	Above substrate	
	Into water column	
Terminus of escape	Under substrate	Predator defense
	Partially under substrate	
	On top of substrate	
Substrate upon which first observed	None      Rock	Habitat selection
	Mud/Grass      Other	
Substrate chosen after escape	Grass      Sedge	Habitat selection, and
	Mud      Old sedge	predator defense
Nearest object within 20 cm	Log      Packed dirt	Habitat selection
	Wood chips      Needles	
Direction of nearest object within 20 m	Below animal	Habitat selection
	Beside animal	
	Above animal	
Depth	cm	All
Distance to nearest neighbor		Intraspecific interaction
Member of a pair of reciprocal nearest neighbors?*	No, yes	Intraspecific interaction
Number of others individual is nearest neighbor to*	0, 1, 2, 3, 4, 5	Intraspecific interaction

\* Indicates variable was generated from recording procedure.

reciprocal nearest neighbors, and the number of others to which an individual is nearest neighbor ultimately proved to be futile.

In addition to the quadrat work, I regularly swam transects over the width and breadth of the lake. During the day I regularly searched the shoreline for emigrating or immigrating salamanders.

Observations in Lost and Scott Lake were qualitative in nature.

## RESULTS

### Individual Movement

The marking exercise provided little information on movement. Only 10 heat branded animals, of 137 marked, were recaptured. They had all moved at least 10 m, but less than 40 m, from the point of release. The thread marked animals all lost their marks quickly. However, one thread from an individual released at the north side was found in the southwest corner, 150 m away; and a west side release thread was found 230 m away on the east side. Apparently there is some individual movement, but the frequency of occurrence is unknown. No immigration or emigration was ever observed.

### Population Age Structure and Density

The percentage of individuals in age classes one, two and three years are illustrated by week in Figure 2. Young-of-the-year were rarely seen, and were not included in the analyses. Each histogram, except the one for the last sample of 1975, represents the aggregate of several nights of observation. Sample sizes range from 19 in the last sample to 203 in the first sample of 1975. The observed age structures for 1973 and early 1975 are quite similar, indicating some degree of stability in the population and consistency in the aging method. The shift towards predominance of older animals in the



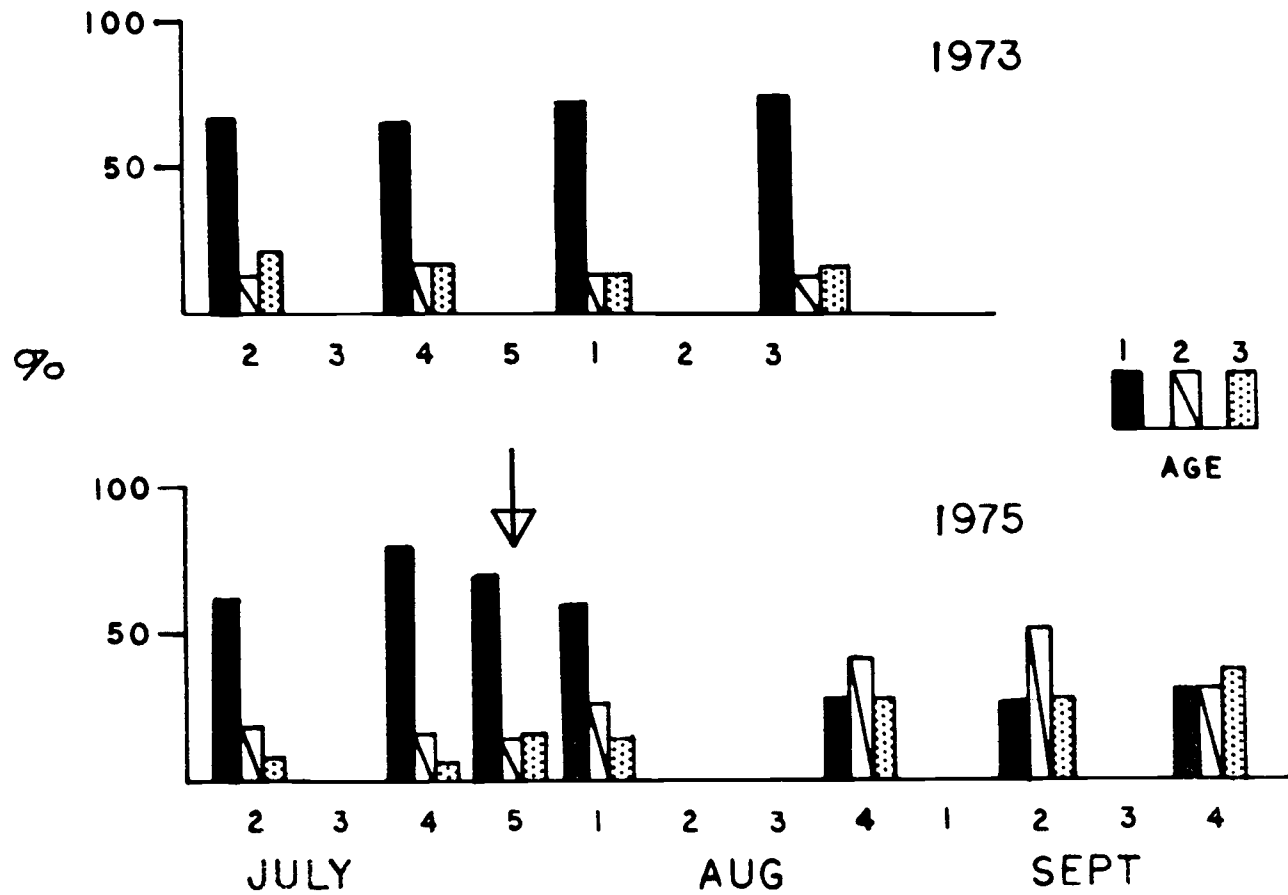


Figure 2. Salamander population age structure, with daily samples lumped by week. Young-of-the-year are not included. Arrow indicates time of 1975 fish stocking.

latter part of 1975 is not a result of growth, as growth rates were allowed for in the aging method. Rather, this shift is evidently the result of increased predation on one-year old animals by the rapidly growing trout fingerlings stocked on 30 July. (This stocking will be referred to hereafter as "the drop.") This sudden increase in predation required the consideration of time before or after the drop in the following analyses. Data for the first week of August are included with the before drop data, as the trout fingerlings were still quite small (80-100 mm in length, probably too small to eat one-year old salamanders) and the age structure was still dominated by one-year old animals.

Densities, as measured by the number of individuals observed within the  $1500 \text{ m}^2$  of quadrat two per night, were about the same from all samples ( $0.04-0.05 \text{ individuals m}^{-2}$ ) in 1973 and early 1975. However, after the drop densities in quadrat two fell to  $0.01-0.02 \text{ individuals m}^{-2}$ . In 1975, densities were approximately the same in quadrats one and two, until the drop. While density fell in quadrat two, it remained unchanged in quadrat one until the very last sample when density fell to  $0.01 \text{ per m}^2$ . The equality of densities in 1973 and early 1975 again indicates some degree of stability in the population, upset by the introduction of fish predators. The difference between densities on quadrats one and two after the drop is probably the result of the fishes' preference for cover; the structural

heterogeneity of quadrat two attracted many new fish (cf. Everest and Chapman, 1972), which then preyed upon the salamanders in that area. As the fish grew, they ate more and more salamanders, with the effect finally showing up on quadrat one. This last result could have been effected by increased foraging by fish along quadrat one, or by salamanders dispersing from quadrat one into areas with reduced densities.

Densities in other sections of the lake differed from those observed within the quadrats, depending upon substrate and depth. Areas of open mud, areas with little habitat structure, and areas deeper than 1 m had fewer salamanders per unit area than did the quadrats. The deepest any northwestern salamanders were seen was 1.3 m; much of the lake, deeper than 1.3 m, was completely devoid of them. It was thus impossible to accurately estimate population size from the density estimates, although there must be at least several hundred salamanders in the lake.

### Habitat Selection

Habitat selection in neotenic northwestern salamanders is for the most part rather subtle. The strongest form of habitat selection is depth preference. As previously stated, no northwestern salamander was found in water deeper than 1.3 m, although I regularly swam transects traversing the length and breadth of the lake, through the

deepest portions. This is consistent with all of my observations from other Cascades lakes. The salamanders do enter deep water to lay eggs, however, as I have found egg masses attached to vegetation in the deepest parts of Fay Lake (4 m), and as deep as 7.5 m in Scott Lake.

The avoidance of deep water restricted the salamanders to the periphery of the lake. Even here there was some form of depth preference, as shown in Figure 3, which illustrates the measured depth positions of all observed animals. While salamanders were found at any depth from 4 to 130 cm, the majority of the animals (63%) positioned themselves at depths between 70 and 100 cm; 75% were found between 60 and 100 cm. The depth distributions are skewed to the left, indicating the strong aversion to deep water, and a lesser aversion to extremely shallow water. If the salamanders randomly selected their positions, one would expect to find them uniformly distributed with respect to depth, since the sloping, non-precipitous bottom of the lake afforded an approximately uniform distribution of depths. The fact that the depth distribution was strongly modal indicates active depth selection. Active depth selection is also indicated by the fact that the depth distribution remained essentially the same over the summer, while the water level fell 1.4 m, and the lake shrank 0.7 ha. To maintain the depth distribution, the animals had to move regularly, or they would have been found in shallower and

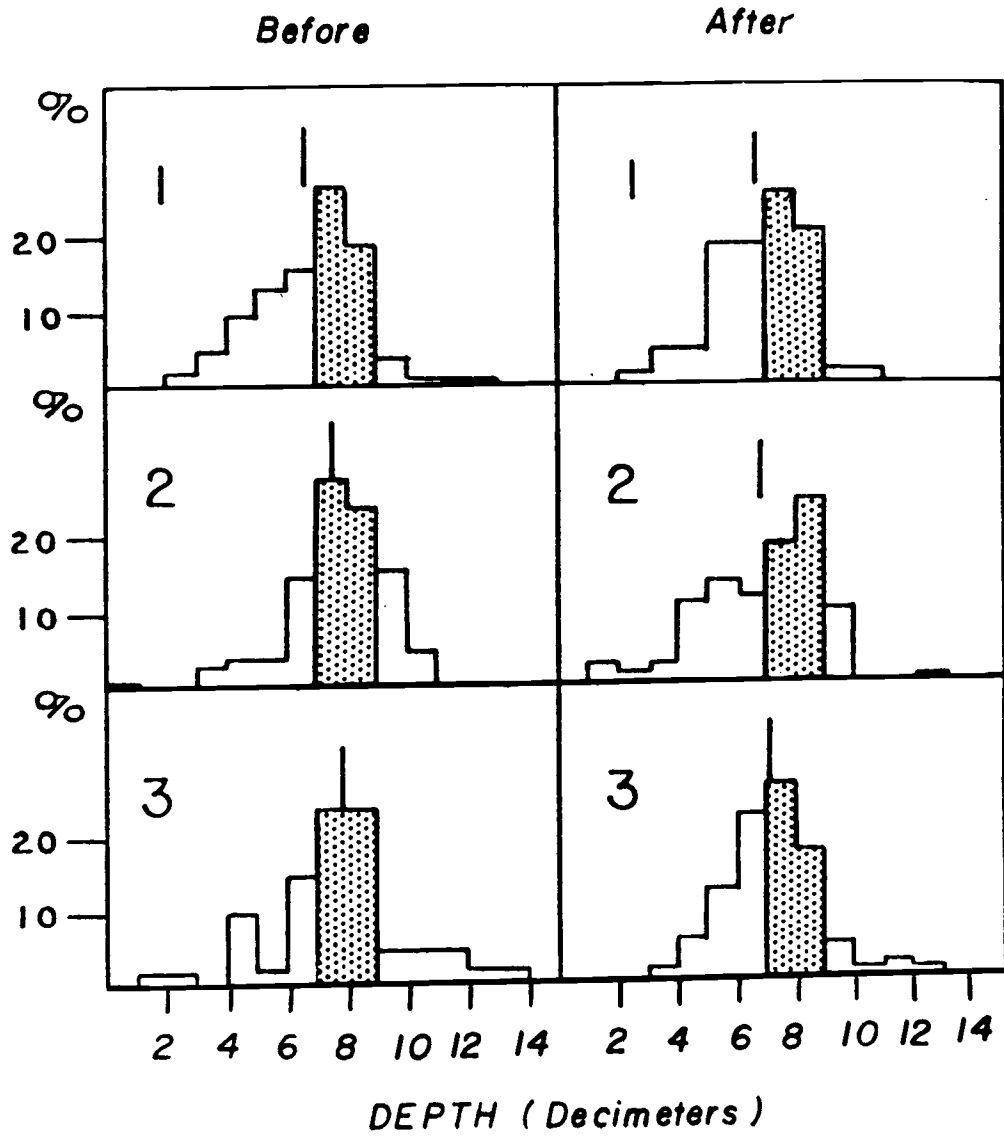


Figure 3. Frequency distribution of depths occupied by salamanders, before and after the drop. Hatched areas indicate frequency of occurrence between 70 and 90 cm. Bars above distributions indicate mean depths.

shallower water. The introduction of new fish had no effect on depth preference.

There are some slight but significant differences in preferred depth between age groups. Although one could find all three age classes at any given depth within the preferred limits, two-year olds tended to occupy deeper positions than did one-year olds ( $p < 0.05$ ), and three-year olds tended to occupy deeper positions than did two-year olds ( $p < 0.025$ , Wilcoxon rank sum test of sample averages). For the entire season one-year olds averaged 67.5 cm, two-year olds averaged 71.6 cm, and three-year olds averaged 74.1 cm in depth. These slight differences probably reflect the relative strengths of deep water avoidance among the age classes, rather than some fine degree of active depth selection.

It is possible that the depth selection was merely the reflection of preference based on some other parameter which varied with depth. However, none of the obvious habitat parameters, temperature, oxygen tension, substrate type or habitat structure, was correlated with depth. In the occupied areas temperatures of both water and substrate surface were usually orthograde, and never varied more than 2°C when measured at the surface of the water and at a depth of 1 m.

I was unable to ascertain much preference in the salamanders for substrate type or habitat structure, as illustrated in Figure 4. The salamanders seemed to have no particular affinity for objects

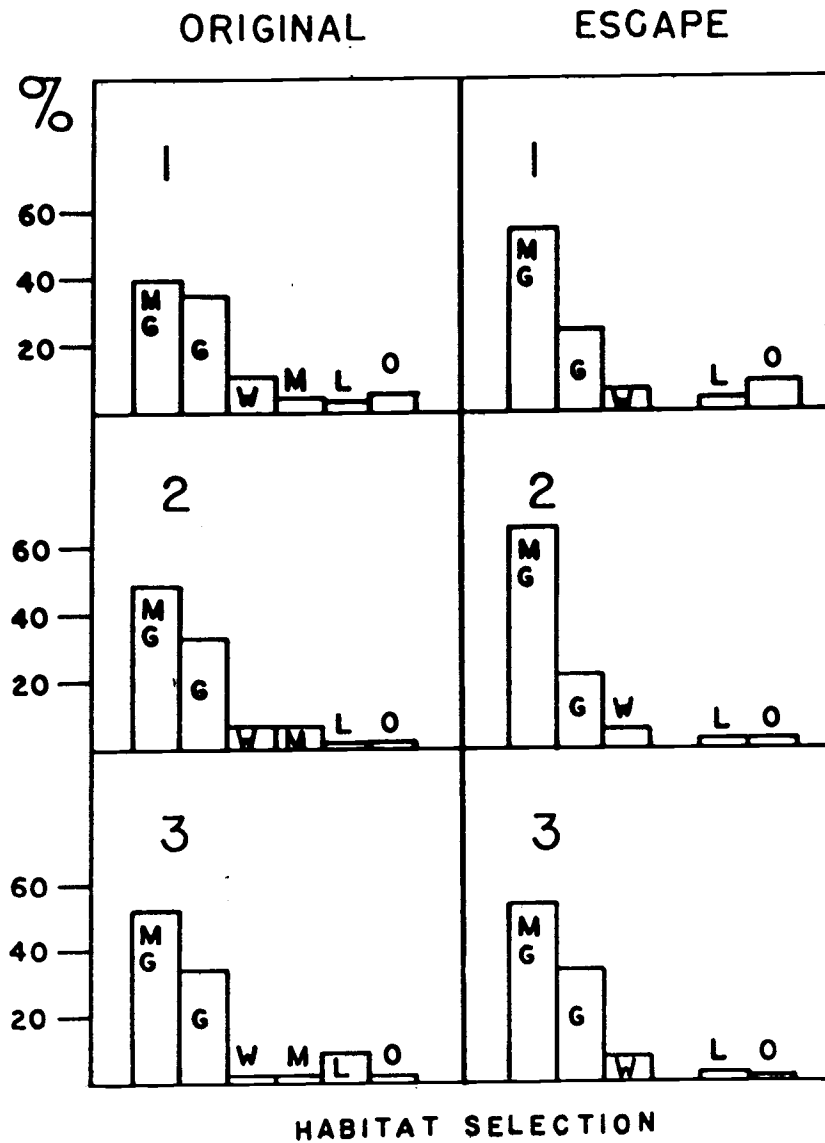


Figure 4. Substrates occupied by salamanders upon original observation, and after escape movement. MG = mud/grass; G = grass; W = wood; M = bare mud; L = log; O = other substrates.

such as logs, sedges, rocks, or aluminum cans which gave vertical structure to the habitat, even when escaping from a noxious stimulus. One exception to this was on quadrat two, where one- and two-year olds occurred on the substrate I called "wood" much more often than would be expected from the frequency in which the substrate type occurred. The "wood" substrate covered less than 2% of the quadrat area, yet a third of the one- and two-year olds in quadrat two were found on it. This substrate comprised manifold small twigs and bark chips sticking up out of the mud to a height of perhaps 8 cm. The mud was normally covered with more bark fragments and conifer needles, but was easily penetrated by the salamanders. The salamanders could have been attracted to this substrate by an abundance of prey items, or they could have been using the emergent twigs as a "cage" to ward off predators. This substrate normally occurred at depths of 60 cm or less.

Another exception to the lack of habitat response of the salamanders was a negative affinity for bare mud. The area composed of this substrate changed weekly due to the combined effects of emerging grass, which reduced the area, and the foot prints of piscators and swimmers, which uprooted the grass and created new areas of bare mud. Salamanders were never found within these footprint craters, even those craters which had been formed over a week previously. They were found in the other areas of bare mud less frequently than



expected on the basis of occurrence of the substrate. Finally, not a single salamander escaped into an area of bare mud. Even those individuals originally positioned on bare mud swam to another substrate type with their escape movement. The salamanders may avoid bare mud because of a dearth of prey in those areas, which I could not detect, or because they are overly conspicuous to predators while on the substrate. The avoidance of this substrate on the escape movement suggests that predators can follow the escape movement into and through the mud, and continue pursuit. Since the slightest vibration will visibly stir up the mud, this last suggestion may obtain.

The salamanders' avoidance of areas deeper than 1.3 m may be based on avoidance of bare mud, since most of the lake deeper than 1.3 m had a bare mud bottom. However, salamanders in Scott Lake also avoid deep water, even though the area deeper than 4 m is heavily vegetated in that lake.

The final case of habitat selection involved a disproportionate amount of escape movement from the grass substrate into the mud/grass type substrate. This is discussed under predator avoidance.

With the three exceptions, the salamanders appeared to be fine grained in their responses to the substrate type and vertical structure. There was no apparent thigmotaxis, nor consistent habitat choice upon escape. The overall picture of substrate preference in northwestern salamanders is that of a generalist making only a little

distinction between any of the substrates upon which it can exist, but avoiding the single substrate lacking vertical structure.

### Predator Avoidance

The behaviors elicited in the escape response, along with the original orientation of the head/body axis, form a sequence of behaviors, any part or group of parts of which may form an adaptive response to attempted predation by fish. That is, an individual choosing a certain alternative or sequence of alternative behaviors when confronted by a predator will escape more often than an individual acting randomly, or choosing a different (wrong) alternative. If such is the case, one would expect that those alternatives forming an adaptive response will occur and be observed more often than expected on a random basis. It is of course possible that two alternatives may be equally advantageous, or an alternative may be advantageous under one set of circumstances and lead to death in another set. The first case of equally advantageous alternatives, when compared to random expectation, will still show deviation due to underrepresentation of the "wrong" behaviors. The second case will show deviation if the circumstances determining advantage are nonrandom, or if the level of resolution of behavioral analysis is fine enough so that the instances of advantage and disadvantage can be considered separately. Otherwise, the frequencies of the alternatives under

different circumstances may be superimposed upon one another to generate spurious conclusions.

If the frequency of occurrence of behavioral alternatives deviates from random expectation of equal probability of occurrence the deviation is prima facie evidence that certain of the alternatives are more advantageous than others. Furthermore, the over- or under-representation of the alternatives, compared to random expectation, is a rough measure of the relative advantage of each. However, such is not necessarily the case for behavioral sequences: the expected frequency of occurrence of two or more behaviors is the product of their individual frequencies of occurrence, but only if the behaviors are independent of each other. If the behaviors are not independent, there is no way of estimating the random probability of occurrence for the sequence. In this case, lack of independence between behaviors indicates that the occurrence of one alternative behavior dictates the relative adaptiveness of the behaviors following or preceding. The interpretation of the lack of independence depends upon the particular behaviors involved. It is still possible to note the relative advantage of different behavioral sequences by noting the over- or underrepresentation of each sequence compared to the expectation derived from the observed frequencies of occurrence of each alternative taken singly.

I have analyzed three components of the escape response for randomness and independence from each other: orientation of the head, direction of escape, and position after the escape movement,

which I call stop position. In addition I have investigated the difference between orientation and direction of escape, which I call shift in position, for independence from orientation and stop position. The behaviors were tabulated by age and time, whether before or after the fish drop. Of course, this partitioning of analysis leads to a multiplicity of significance testing, increasing the probability of both type I and type II logical errors.

Analysis of the escape response also involved a fourth variable, the height of the escape movement above the substrate. In 1973, approximately 11% of all salamanders approached swam up into the water column while escaping, a movement that made them very easy to net. Another 9% swam about 5 cm above the substrate, while the rest essentially hugged the surface of the substrate while escaping. In 1975 there was virtually no variation in this behavior: only 1 salamander of 726 observed escaped into the water column; only 22 exceeded a height of 3 cm above the substrate while darting away. Apparently there was strong selection against any movement which takes the animal very far above the substrate.

My final analysis of predator avoidance behavior involved checking for significant association of the behaviors with the depth of water at the position chosen by each individual.

Table 2 lists the observed numbers of occurrence of the three alternatives of head orientation, and compares them by Chi-Square

Table 2. Orientation of head, chi-square test of randomness, 2 DF. Random expectation = proportion of 1 toward shore (S): 2 lateral (L): 1 toward deep water (D).

Orientation	Before Drop			After Drop			Total		
	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>
<u>Age 1</u>									
S	80	70	1.51	13	15	0.27	93	85	0.80
L	117	140	3.63	31	30	0.03	148	170	2.73
D	82	70	<u>1.65</u>	16	15	<u>0.07</u>	98	85	<u>2.07</u>
Total			6.79*			0.37 ns			5.60 ns
<u>Age 2</u>									
S	12	20	2.89	29	26	0.41	41	45	0.40
L	42	39	0.23	41	52	2.14	83	91	0.62
D	24	20	<u>1.04</u>	33	26	<u>2.04</u>	57	45	<u>3.05</u>
Total			4.15 ns			4.59 ns			4.07 ns
<u>Age 3</u>									
S	8	11	0.82	18	16	0.40	26	27	0.01
L	19	22	0.41	24	31	1.58	43	53	1.89
D	17	11	<u>3.27</u>	20	16	<u>1.31</u>	37	27	<u>4.16</u>
Total			4.50 ns			3.92 ns			6.05*

ns = not significant.

\* = p < 0.05.

test with the frequencies expected if the behavior is random. Since there are four quadrants of orientation, one would expect a proportion of one oriented towards shore : two oriented laterally : one oriented towards deep water, if a salamander is as likely to face one direction as another. One-year old animals deviated significantly from this proportion before the drop, but matched it almost perfectly after the drop. Two and three-year olds did not significantly deviate from this proportion. However, in all cases there was an overrepresentation of deep water orientation, and in all but two cases, an underrepresentation of lateral orientation. This tendency was especially noticeable in three year olds: when the observations are lumped for the entire summer, the deviation is statistically significant. The advantage of orienting toward deep water may lie in early detection of large fish, which are most often found in deep water. However, the actual advantage is probably more complex, involving several components of the escape response. The change from nonrandom to random orientation in one year olds could be the result of sampling error in either sample. However, I believe that the change reflects a biological phenomenon: fingerling fish are as likely to come from one quadrant as another; after the drop, therefore, no orientation is more advantageous than another, at least for the small one year old animals most susceptible to harassment by fingerling fish. The randomness of behavior in two year olds is quite consistent with their other

behaviors, as will be shown.

In addition to the tendency to orient toward deep water and not laterally, in three-year olds there is a consistent association of depth with orientation: animals that orient toward deep water occupy positions in significantly deeper water than do animals that orient toward shore. (Before and after drop samples combined, Wilcoxon rank sum test of sample averages,  $p < 0.05$ .) This indicates that at least some members of this size class are aware of their position with respect to lake structure. The exact adaptive basis of this association is not apparent in the behavior taken alone, but may be manifest by consideration of the entire escape sequence. There was no consistent relationship with depth for those individuals orienting laterally.

Table 3 lists the frequencies for the alternatives of direction of escape, compared to the same null hypothesis of a 1:2:1 proportion. One- and two-year old animals showed the same relationship to randomness as observed in orientation. This is due to the lack of independence between orientation and direction of escape, demonstrated below. In the three year olds, the tendency to avoid the lateral quadrants was much stronger than it was in orientation, strong enough to produce a significant deviation from randomness.

Table 4 depicts the results of the tests of independence between orientation and direction of escape. In one- and two-year olds, there is a highly significant lack of independence between the two behaviors,

Table 3. Direction of escape, chi-square test of randomness, 2 DF. Random expectation = proportion of 1 toward shore (S): 2 Lateral (L): 1 toward deep water (D).

Direction	Before Drop			After Drop			Total		
	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>
<u>Age 1</u>									
S	87	70	4.27	19	15	1.07	106	85	5.33
L	113	140	5.03	24	30	1.20	137	170	6.23
D	79	70	<u>1.23</u>	17	15	<u>0.27</u>	96	85	<u>1.49</u>
Total			10.53**			2.54 ns			13.05**
<u>Age 2</u>									
S	21	20	0.12	28	26	0.25	49	45	0.36
L	35	39	0.41	50	51	0.02	85	90	0.28
D	22	20	<u>0.32</u>	24	26	<u>0.09</u>	46	45	<u>0.02</u>
Total			0.85 ns			0.36 ns			0.66 ns
<u>Age 3</u>									
S	17	11	3.63	23	16	3.63	40	26	7.20
L	8	22	8.48	21	31	3.23	29	53	10.52
D	18	11	<u>4.89</u>	18	16	<u>0.40</u>	36	26	<u>3.62</u>
Total			17.00**			7.26*			21.34**

ns = not significant.

\* = p < 0.05.

\*\* = p < 0.01.



Table 4. Independence of direction of escape from original orientation of head. 3 x 3 contingency table, chi-square with 4 DF. S = towards shore, L = laterally, D = towards deep water.

Orientation	Direction	Before Drop			After Drop			Total		
		Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>
<u>Age 1</u>										
S	S	53	25	31.50	8	4	3.66	61	29	35.04
S	D	7	23	10.80	2	4	0.77	9	26	11.41
S	L	20	32	4.75	3	5	0.93	23	38	5.66
L	S	30	36	1.15	11	10	0.14	41	46	0.60
L	L	62	47	4.51	15	12	0.55	77	60	4.94
L	D	25	33	1.99	5	9	1.63	30	42	3.39
D	L	31	33	0.15	6	6	0.03	37	40	0.17
D	S	4	26	18.20	0	5	5.07	4	31	23.17
D	D	47	23	<u>24.36</u>	10	5	<u>6.59</u>	57	28	<u>30.82</u>
Total				97.40**			19.37**			115.20**
<u>Age 2</u>										
S	S	9	3	10.30	17	8	11.29	26	11	20.97
S	D	0	3	3.38	1	7	4.74	1	10	8.32
S	L	3	5	1.06	10	14	1.01	13	19	1.84
L	S	12	11	0.04	10	11	0.14	22	23	0.02
L	L	20	19	0.07	23	20	0.42	43	39	0.37
L	D	10	12	0.29	8	10	0.28	18	21	0.49
D	L	12	11	0.14	17	16	0.04	29	27	0.16
D	S	0	6	6.46	1	9	7.17	1	16	13.58
D	D	12	7	<u>4.04</u>	15	8	<u>6.75</u>	27	15	<u>10.61</u>
Total				25.78**			31.83**			56.35**

Table 4. Continued.

Orientation	Direction	Before Drop			After Drop			Total		
		Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>
<u>Age 3</u>										
S	S	6	3	2.55	11	7	2.80	17	10	5.08
S	D	1	3	1.65	2	5	1.99	3	9	3.92
S	L	1	1	0.16	5	6	0.20	6	7	0.19
L	S	9	7	0.50	8	9	0.09	17	16	0.63
L	L	4	3	0.13	9	8	0.04	13	12	0.17
L	D	5	8	0.85	7	7	0.00	12	14	0.40
D	L	3	3	0.01	7	7	0.01	10	10	0.00
D	S	2	7	3.32	4	7	1.58	6	14	4.65
D	D	12	7	<u>3.35</u>	9	6	<u>1.76</u>	21	13	<u>5.45</u>
Total		12.52*			8.47 ns			19.94**		

ns = not significant.

\* = p < 0.05.

\*\* = p < 0.01.

due to a propensity for going straight ahead when startled. This propensity was demonstrated by the large overrepresentation of animals escaping in the same direction as originally oriented, when the orientation was not lateral. There was a consistent underrepresentation of reversals in direction. This lack of independence accounts for the results for these groups shown in Table 3: the results in Table 3 are merely the reflection of the results in Table 2. Age three animals also showed a general lack of independence between orientation and direction of escape. The results for after the drop are best interpreted as a type II error. (i. e. , The behaviors are not independent, but sampling error prevents rejection of the null hypothesis of independence. )

One can understand the relationship between orientation and the escape movement better by looking at direction of escape in a slightly different manner, as shift between the quadrants of orientation and direction of escape. This shift can have a value of zero (animal goes straight ahead), one (a right angle turn), or two (reverse direction). (n. b. A single individual of each age class rotated three quadrants while escaping; these individuals were not included in the analysis.) Independence between shift and orientation is summarized in Table 5. The levels of Table 5 are very similar to those of Table 4: SS of Table 4 corresponds to S0 of Table 5, likewise SL = S1, SD = S2, DD = D0 , DL = D1, and DS = D2; LD and LS of Table 4 are

Table 5. Independence of shift in direction of escape, from orientation of head. 3 x 3 contingency table, chi-square with 4 DF. S = towards shore, L = laterally, D = towards deep water; 0 = 0°, 1 = 90°, 2 = 180°.

Orientation	Shift	Before Drop			After Drop			Total		
		Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>
<u>Age 1</u>										
S	0	53	46	1.11	8	7	0.10	61	53	1.22
	1	20	30	3.55	3	5	1.05	23	36	4.66
	2	7	4	2.87	2	0	0.55	9	4	5.80
L	0	60	67	0.75	15	17	0.24	75	84	1.02
	1	55	44	2.50	16	13	0.74	71	57	3.33
	2	2	5	2.18	0	1	1.10	2	7	3.16
D	0	47	47	--	10	9	0.16	57	56	0.03
	1	31	31	--	6	7	0.07	37	38	0.02
	2	4	4	<u>0.01</u>	0	1	<u>0.55</u>	4	4	<u>0.03</u>
Total				12.98*			4.56 ns			19.27**
<u>Age 2</u>										
S	0	9	6	1.50	17	15	0.24	26	21	1.25
	1	3	6	1.27	10	12	0.45	13	18	1.50
	2	0	0	0.31	1	1	0.37	1	1	0.01
L	0	18	21	0.43	23	22	0.04	41	43	0.13
	1	22	20	0.22	18	18	--	40	38	0.13
	2	2	1	0.79	0	1	0.80	2	2	0.01
D	0	12	12	--	15	18	0.44	27	30	0.26
	1	12	11	0.03	17	15	0.41	29	26	0.35
	2	0	1	<u>0.62</u>	1	1	<u>0.19</u>	1	1	<u>0.06</u>
Total				4.86 ns			2.94 ns			3.70 ns

Table 5. Continued.

Orientation	Shift	Before Drop			After Drop			Total		
		Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>
<u>Age 3</u>										
S	0	6	4	1.12	11	9	0.61	17	12	1.72
	1	1	3	1.65	5	8	1.19	6	11	2.37
	2	1	1	0.09	2	2	0.04	3	2	0.11
L	0	3	9	3.81	9	12	0.58	12	20	3.20
	1	14	8	5.55	15	10	1.98	29	18	6.72
	2	1	2	0.27	0	2	2.32	1	4	2.25
D	0	12	8	1.65	9	9	0.01	21	18	0.32
	1	3	7	2.38	7	9	0.33	10	16	2.16
	2	2	2	<u>0.11</u>	4	2	<u>2.20</u>	6	4	<u>1.70</u>
Total				16.62**			9.27 ns			20.61**

ns = not significant.

\* = p < 0.05.

\*\* = p < 0.01.

combined to form L1 of Table 5, and LL is broken down into L0 and L2. However, the results are surprisingly different. Shift was independent of orientation in two-year olds, and in one-year olds after the drop. This means that while these groups do have a propensity for escaping straight ahead, which produces the lack of independence between orientation and direction of escape, this propensity and the converse likelihood of turning 90 or 180 degrees are the same no matter what the original orientation. The animals in these groups appear to be entirely random in their choice of orientation and direction, or rotation, for escape.

In three-year olds, and one-year olds before the drop, the lack of independence in shift clarifies the lack of independence in direction of escape. (I consider the Chi-square for the three year olds after the drop again to reflect a type II error.) In these animals, there is a propensity for going straight ahead to escape, if the individual is facing towards shore or deep water; there is a strong propensity for turning to escape if the individual is facing laterally. This nonrandom escape behavior thus has two components: a tendency to face towards deep water, or at least not laterally; and a tendency to avoid moving laterally when startled, which is itself composed of two components based on the original orientation. This again strongly suggests that some individuals in these groups are aware of the physical structure of the lake, and their position with respect to that structure.

Direction of escape in three-year olds is also associated with depth. Figure 5 illustrates the mean depths of those individuals utilizing escape towards shore, and towards deep water, for each sample. Three-year olds which escape towards deep water consistently tenanted deeper water than did those which escaped towards shore. This difference in depth is statistically significant (Wilcoxon rank sum test of sample means,  $p = 0.01$ ), and slightly more consistent than in the affinity of depth with orientation to which it is related. The main component of this depth relationship is the propensity for escaping straight ahead, if oriented towards shore or deep water, which then reflects the previously observed association between orientation and depth. However those three-year olds that oriented laterally, but escaped towards deep water also occupied deeper water more often than did their laterally oriented, shoreward escaping fellows (Mann-Whitney U test of original variates,  $p < .10$ ). This tendency was not as strongly developed as it was in those individuals originally avoiding lateral orientation. Those three-year olds escaping laterally showed no consistent depth relationship, nor did one- or two-year olds.

The adaptive basis of orientation and direction of escape in three year olds is now discernible. First of all, escaping straight ahead when attacked by a predator is usually most adaptive because this behavior puts the greatest distance between the salamander and

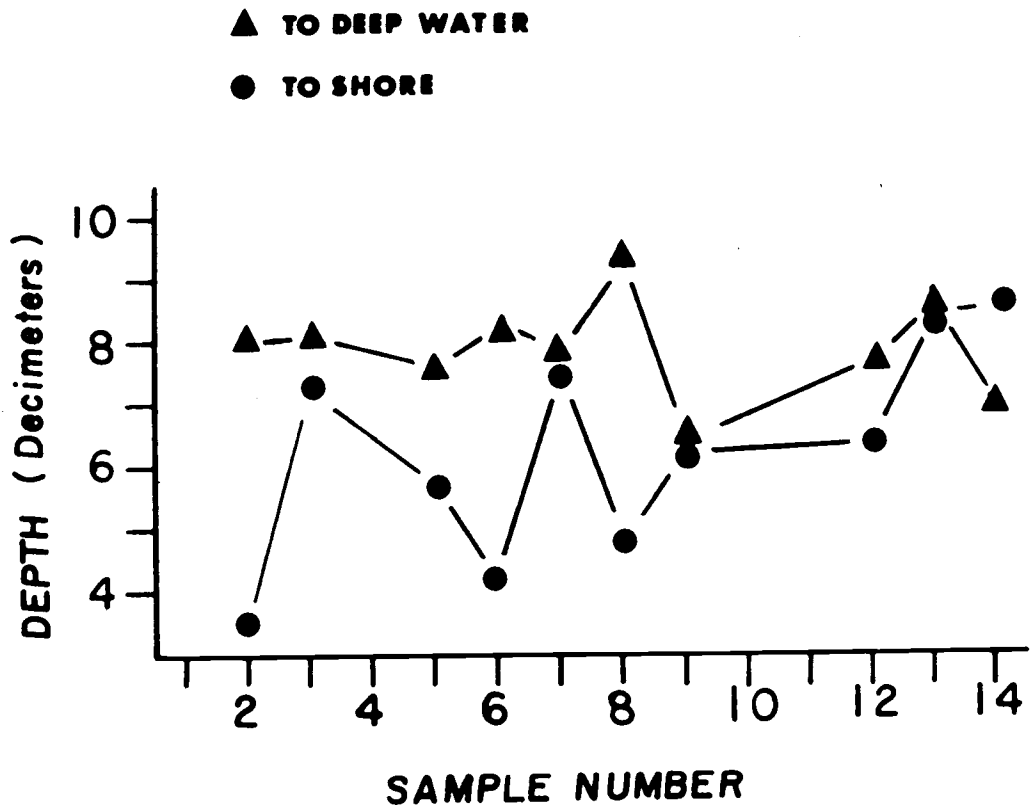


Figure 5. Average depth occupied by three-year-olds that escaped toward deep water, and those that escaped toward shore.



the predator in the shortest period of time. No time is lost in turning, or in any movement which lengthens the straight line distance between the original position and the stop position. However, if fish most often move in and out from deep water, then this response is adaptive for a laterally oriented animal only if it allows the predator to close upon it. If the salamander initiates the response while the predator is still distant, then in escaping at right angles to the predator's approach it increases its distance from the predator in proportion to the sine of the angle formed by the shore-deep water axis and the line between it and the predator. Since the sine of an angle is always less than one (unless the angle is  $90^\circ$ , which means that the predator is on top of the prey), the salamander is moving less than a unit away from the predator for each unit of actual movement. In other words, it is moving more slowly in relation to the predator than it would be if it swam directly toward or away from the predator. The further away the predator is at the initiation of the escape movement, the slower the right angle get-away. If getting away from a predator rapidly is important for survival, then moving at right angles to the approach of a predator is not a good way to survive. This size group, then, tends to orient in a direction allowing the quickest straight line escape upon the approach of a predator. If an animal happens to be oriented laterally, however, a quick turn and escape along the shore/deep water axis may permit more rapid escape than

moving straight ahead, at right angles to the axis.

A simplifying assumption can explain the association of depth with behavior, also. If a predator approaches most often from deep water, then there are two logical alternatives of escape action for a prey: move out of the perceptual field of the predator, so that it can no longer locate the prey; or move into an area into which the predator is reluctant to follow. Perhaps the quickest way to move out of the perceptual field of a fish is to rapidly move towards and under it. As soon as the salamander passes underneath the fish, it at least moves out of the fish's visual field, vision being a major part of a fish's perceptual apparatus, even in dim light (Ivlev, 1961). The escape movement itself, just along the surface of the substrate, is ideal for such an escape, especially if the salamander buries itself in the substrate upon passing out of the predator's perception. Thus three-year olds in deeper positions (greater than 70 cm deep) may well avoid predation best by rapidly moving toward deep water when attacked. Their fellows in shallow water (less than 70 cm) may avoid predation best by moving straight ahead into even shallower water, where their escape path is masked by greater habitat structure, and/or where the fish are reluctant to follow. There is some evidence that stream trout older than one year avoid shallow water (Everest and Chapman, 1972).

The one-year olds before the drop showed essentially the same behavior as the three-year olds, with a stronger avoidance of lateral orientation, and without the association of depth with behavior. Apparently this age group, under relatively low predator pressure, is principally dependent upon rapid escape to avoid predation. After the drop, escape behavior became essentially random. As mentioned before, this change in behavior could be the result of increased harassment and predation by the fingerlings dropped in July. Griffith (1972) found that underyearling cutthroat trout in streams chose to occupy shallow water (mean depth 26 cm) and also chose to remain close to cover (mean distance from cover, 12 cm) which in Fay Lake is found around the periphery, next to shore. These fingerlings are as likely or more likely to come from shallow water or a lateral direction as they are to come from deep water. The combined predatory movement of all fish is then essentially unpredictable, with large fish coming from deep water and fingerlings from every other direction. Thus no particular salamander behavioral sequence provides more escape from fish than any other for one year olds.

The third behavior in the escape response is the stop position, with two clearcut alternatives: under and on top of the substrate. Like the proverbial ostrich, a few individuals of each age class embedded themselves in the substrate leaving some part of their body exposed. Since these animals apparently had the inclination to burrow

into the substrate, but achieved essentially the same position as if they had chosen to remain on top of the substrate, they were not included in the analysis of stop position.

Table 6 shows that the majority of individuals of all ages went into the substrate when startled. This predilection was weakly developed in two- and three-year olds before the drop, becoming much more dominant after the drop. (The Chi-square value for two-year olds is actually not significant. However the association of depth with this behavior, discussed below, and the fact that the trend is the same as in the other age classes indicates that at least some individuals are acting nonrandomly.) This increase in the frequency of one alternative is probably the result of increased harassment by fingerlings. The strong development of the trait in one year olds before the drop indicates that stop position is important for this age group, even at relatively low predator density. It is not surprising that the majority of animals chose to escape into the substrate. At least superficially, this would appear to be an excellent way of escaping from a predator, given the alternative of remaining in the open.

The inclination to seek cover under the substrate is independent of orientation, direction of escape, or shift in direction. The exception to this is the orientation of one year olds, as shown in Table 7. There was a tendency for individuals in this age class that orient toward shore to go under the substrate more often than expected;

Table 6. Position at end of escape responses, chi-square test for randomness, 1 DF. Random expectation = proportion of 1 under substrate (U); 1 on top of substrate (O).

Position	Before Drop			After Drop			Total		
	Observed	Expected	$X^2$	Observed	Expected	$X^2$	Observed	Expected	$X^2$
<u>Age 1</u>									
U	165	137	5.72	48	30	11.60	213	167	12.99
O	109	137	<u>5.72</u>	11	30	<u>11.60</u>	120	167	<u>12.99</u>
Total			11.45**			23.20**			25.97**
<u>Age 2</u>									
U	44	39	0.79	77	51	13.25	121	90	11.09
O	33	39	<u>0.79</u>	25	51	<u>13.25</u>	58	90	<u>11.09</u>
Total			1.57 ns			26.51**			22.17**
<u>Age 3</u>									
U	26	20	1.80	48	31	9.32	84	56	14.00
O	14	20	<u>1.80</u>	14	31	<u>9.32</u>	28	56	<u>14.00</u>
Total			3.60 ns			18.65**			28.00**

ns = not significant.

\* =  $p < 0.05$ .

\*\* =  $p < 0.01$ .

Table 7. Independence of stop position from orientation. 2 x 3 contingency table, chi-square with 2 DF. U = under substrate, O = on top of substrate; S = towards shore, L = laterally, D = towards deep water.

Position	Orientation	Before Drop			After Drop			Total		
		Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>
<u>Age 1</u>										
U	S	55	48	0.97	13	11	0.56	68	59	1.22
	L	66	68	0.06	26	24	0.10	92	91	0.00
	D	44	49	0.47	9	13	1.24	53	62	1.32
O	S	25	32	1.46	0	2	2.42	25	34	2.16
	L	47	45	0.09	4	6	0.45	51	52	0.01
	D	37	32	<u>0.71</u>	7	3	<u>5.40</u>	44	35	<u>2.34</u>
Total				3.76 ns			10.18**			7.05*
<u>Age 2</u>										
U	S	4	7	1.19	19	21	0.22	23	27	0.60
	L	26	24	0.17	33	31	0.14	59	56	0.15
	D	14	13	0.06	25	25	0.00	39	38	0.03
O	S	8	5	1.59	9	7	0.67	17	13	1.26
	L	16	18	0.22	8	10	0.42	24	27	0.31
	D	9	10	<u>0.07</u>	8	8	<u>0.00</u>	17	18	<u>0.07</u>
Total				3.29 ns			1.44 ns			2.43 ns
<u>Age 3</u>										
U	S	5	5	0.04	15	14	0.08	20	18	0.19
	L	10	11	0.10	17	19	0.13	27	30	0.25
	D	11	10	0.03	16	15	0.02	27	26	0.03
O	S	2	2	0.08	3	4	0.28	5	7	0.51
	L	7	6	0.18	7	5	0.46	14	11	0.67
	D	5	6	<u>0.06</u>	4	5	<u>0.06</u>	9	10	<u>0.08</u>
Total				0.51 ns			1.03 ns			1.72 ns

ns = not significant.

\* = p < 0.05.

\*\* = p < 0.01.

individuals facing deep water stayed out more often than expected. The statistical significance after the drop is based on the deviation of only four animals, but the trend was the same before the drop. The interpretation of this association between orientation and the two alternatives is obscure, if indeed the association really exists.

While stop position is principally independent of the behavior preceding it, it is not independent of depth for one- and two-year olds. Figure 6 shows the average depths of individuals choosing to go under or stay on top of the substrate, for each of the nights of observation. In one- and two-year olds, those individuals choosing to escape into the substrate consistently occupied deeper water than did the individuals remaining on top. That is, individuals in deeper water tended to go under the substrate, while individuals in more shallow water tended to remain out when startled. This difference in depths associated with the two alternatives is statistically significant for both one- and two-year olds (Wilcoxon rank sum test of sample means,  $p < 0.005$  for both ages).

One possible interpretation of this phenomenon is that individuals with the inclination to escape under the substrate also have the inclination to choose deeper water than do those individuals choosing the alternative. Another interpretation states that most individuals are aware of the depth of their position, and accordingly choose the stop position appropriate for that depth. Either interpretation implies that

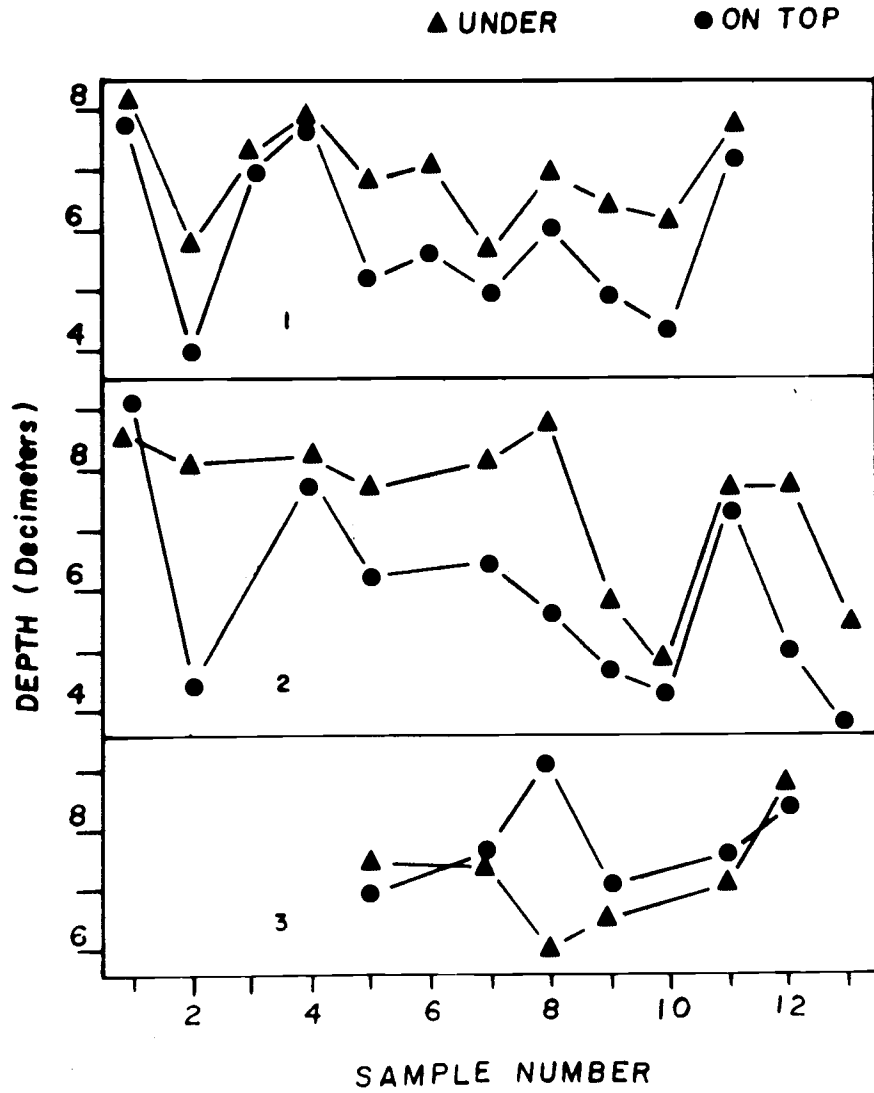


Figure 6. Average depths occupied by salamanders that burrowed under the substrate, and by those that remained on top of the substrate, at the end of the escape movement.



the salamanders are aware of depth, an implication of most of the other data, but there is no criterion for choosing between the two, other than Occam's razor: the latter interpretation requires that each individual recognize both behavioral alternatives, and have the ability to choose the correct one. The first interpretation only requires that each individual recognize a single alternative, which happens to be appropriate for the depth which it also chooses. Exactly why the alternatives are appropriate for different depths is also obscure. Habitat structure decreases with depth, and it is possible that in shallow water the animals blend into the structure upon escape, while in deeper water only complete submergence will hide an animal. Alternatively, the greater habitat structure in shallow water may preclude passage into the substrate (i. e. , grass or sedge roots offer more resistance to penetration in the shallows, where they grow more densely). There is some evidence for this in the fact that a disproportionate number of salamanders originally positioned on the grass substrate chose to escape to the less densely vegetated mud and grass type substrate (see Figure 4). From an energetics view point, remaining on the substrate surface should require less energy than seeking cover underneath, and therefore may be advantageous under those conditions in which either alternative permits escape from predators. Invoking the previously stated assumption that fish are reluctant to enter water of less than a certain depth increases the

appeal of this hypothesis. It is also possible that in some substrates (e. g. , bare mud), burrowing into the substrate may leave a trail of disturbed particles which a predator could follow. Whatever the basis of the behavior, I submit that remaining on top of the substrate after escape can be appropriate under some conditions.

The three-year olds did not show any consistent association of stop position with depth. This age group apparently has sufficient programmed behavior prior to the end of the escape movement such that depth is not an important determinant of the propriety of a stop position. Three-year olds showed the least proclivity for remaining on the substrate surface, which indicates that going underneath the substrate may be the appropriate stop position for them under most conditions. Perhaps the one in four which do remain on top have never met a predator which could collect the wages of their sin.

#### Aggregation and Social Interaction

The salamanders are obviously aggregated when considered on the scale of the entire lake, since much of the lake is entirely devoid of northwestern salamanders. Furthermore, densities vary between different areas which are inhabited by the salamanders, creating a clumped dispersion on the scale of suitable habitat. At the scale of the transects, the dispersion pattern was not so qualitatively obvious, and required quantification for description.

On the transects the positions of observed animals were frozen into a pattern with marked flags. The dispersion of this pattern could then be distinguished by analysis of the distances between the salamanders and their nearest neighbors. Table 8 presents this analysis, using Clark and Evans' (1954) method of detecting deviation between the average nearest neighbor distance and that expected on the basis of random dispersion. Here  $R$  is the ratio of the observed to expected nearest neighbor distances. This ratio should equal one for random dispersions, and should be less than one for aggregated dispersions. The  $z$  score tests the deviation between the observed ratio and unity, expressed as a standard normal deviate. Values of  $z$  less than  $-2.33$  indicate that the deviation from random, towards aggregation, is significant with a probability  $<0.001$ .

One problem in determining nearest neighbor distances was the occurrence of individuals whose nearest neighbor was more than 2.6 m away (2.6 m was the maximum length of measuring stick I could handle underwater). The inclusion of these "loners" in the analysis would obviously increase the average nearest neighbor distance, pushing characterization of the dispersion towards random. However, if one assumes that most of the loners occurred on the lateral edges of the transect (i. e. , their nearest neighbor was actually outside the transect, and their true nearest neighbor distance was not properly part of the sample), their occurrence can be ignored and the observed

Table 8. Intrapopulation dispersion, as measured by nearest neighbor distances. The average distance expected, assuming a random dispersion, is compared to the observed average distance, using the method of Clark and Evans (1954). The ratio,  $R$ , of observed to expected should equal unity for a random dispersion;  $Z$ -scores of less than  $-2.33$  indicate aggregation with a probability  $> 0.999$ .

Date	Quadrat Number	N	Expected Average Distance	Observed Average Distance	$R = \frac{\text{Observed}}{\text{Expected}}$	Z
<u>1973</u>						
7/18	2	34	194 cm	71 cm	0.37	-7.26
8/29	1	48	194	55	0.28	-9.72
<u>1975</u>						
7/10	1	47	194	65	0.34	-8.98
7/11	2	18	194	71	0.37	-5.94
7/23	1	51	192	59	0.31	-9.47
7/24	1	40	194	74	0.38	-7.86
7/30	1	34	194	126	0.65	-4.59
7/31	2	46	194	65	0.34	-9.00
8/4	1	41	194	84	0.43	-7.66
8/5	2	45	194	104	0.54	-6.26
8/24	1	46	194	97	0.50	-6.78
8/25	2	12	343	150	0.44	-4.31
8/25	1	23	194	121	0.63	-4.10
9/8	1	46	185	103	0.56	-6.23
9/9	2	13	280	135	0.48	-4.65
9/9	1	15	259	97	0.38	-5.60
9/23	2	3	484	101	0.21	-4.28
9/23	1	4	413	135	0.33	-4.27

averages taken as reasonable estimates. I believe that this assumption is entirely justified. However, the occurrence of these loners did prevent me from using an alternate method of determining dispersion, to wit, comparing the number of pairs of reciprocal nearest neighbors to random expectation.

The data from all transects, for both years of observation, indicate strong aggregation among the salamanders: the presence of one salamander is a good predictor of the presence of another nearby. Conversely, there are large areas within the study quadrats which are devoid of salamanders.

Since there is depth preference among the salamanders, an obvious basis of aggregation is simple congregation within the quadrats, in areas near the preferred depth. However, this situation necessarily implies that individuals in deeper water are more distant from their neighbors than are those individuals in the shallower, more preferred areas. One must also expect loners to occur most often in deeper water, in violation of the assumption stated above. Such is not the case: 72% of the loners occurred in the preferred depth zone of 60-100 cm, against 75% of the total population. To further test for correlation between depth and nearest neighbor distance, I conducted a multiple regression analysis of nearest neighbor distance. The addition of the depth variable to the regression model did not significantly add to the precision of the model. Therefore I

cannot accept the hypothesis that animals in deeper water are spaced out to a greater degree than are those in shallower water. The aggregation is not produced by a mere thinning out of animals with depth, and apparently is not dependent upon depth at all.

The clumping behavior is dictated by a number of factors, including dispersion of prey and habitat selection, although none of these factors are glaringly apparent. The most obvious component of aggregation is the previously mentioned avoidance of bare mud substrate by all age classes, and the affinity of one- and two-year olds for the "wood" substrate. This habitat selection concentrated the salamanders in some areas, while few were found in the areas covered with bare mud. However, examination of the age structure of the nearest neighbor patterns uncovers two other important components of aggregation. Table 9 compares the observed numbers of age specific individual and nearest neighbor pairs with the numbers expected if the animals are randomly associated. One-year olds with one-year old neighbors were strongly overrepresented; one-year olds with older neighbors were underrepresented. Two- and three-year olds, on the other hand, have more two- and three-year old neighbors than expected on a random basis. This indicates that either one-year olds strongly avoid association with older animals or that all salamanders tend to associate with other individuals of about the same size. The observed aggregation apparently involves both tendencies. Since there

Table 9. Independence of individual age from age of nearest neighbor. Chi-square test with 4 DF.

Neighbor Age	Before Drop			After Drop			Total			
	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>	Observed	Expected	X <sup>2</sup>	
<u>Age 1</u>										
1	197	181	1.34	11	6	3.67	208	155	18.09	
2	26	38	3.67	20	19	0.02	46	78	13.37	
3	17	21	0.67	5	10	2.84	22	43	9.96	
<u>Age 2</u>										
1	31	41	2.37	14	13	0.04	45	74	11.11	
2	14	9	3.56	38	41	0.27	52	37	5.89	
3	9	5	4.02	25	22	0.32	34	20	9.40	
<u>Age 3</u>										
1	17	23	1.42	3	8	3.53	20	44	13.39	
2	11	5	8.35	29	26	0.27	40	22	13.76	
3	2	3	<u>0.14</u>	17	14	<u>0.54</u>	19	12	<u>3.80</u>	
Total			25.53				11.51			
			p < .005				p < .03			
								98.76		
								p < .005		

is a significant positive correlation of age with depth, one would expect one age class to predominate at a given depth, and thus most individuals at that depth would have a nearest neighbor of the same age. Age-specific habitat selection can lead to aggregation. It is not the only component of the clumping behavior, however. Before the drop, when the one-year olds were quite small, their association with two-year olds was strongly underrepresented. After the drop, when one-year olds were closer to the two-year olds in size, there was no such underrepresentation. The underrepresentation of one-year olds with three-year old neighbors remains about the same through time. Clearly, small one-year olds avoid all larger animals. As they grow, their avoidance of the next largest size class disappears, and as they age into two-year olds all avoidance behavior disappears. It is evident that there is an element of social interaction involved in clumping behavior, namely avoidance of large animals by small ones. Whether or not there is an active attraction between animals of similar size and age, as opposed to the passive attraction induced by mutual depth preference, is a yet unanswered question.



## DISCUSSION

Trout are effective predators on larval and neotenic ambystomatid salamanders. Burger (1950) observed that neotenic Ambystoma tigrinum nebulosum disappeared from Emerald Lake, Colorado, after the introduction of trout into the lake. Sprules (1974) found that this subspecies occurred as a neotene only in ponds into which fish had never been introduced, and hypothesized that in general paedogenesis in ambystomatids could evolve only in waters lacking a predatory fish fauna. In a quick study in British Columbia, he found that A. gracile neotenes were on the average 16 times more abundant in lakes with no fish than they were in lakes into which fish had been introduced. Efford and Mathias (1969) noted that trout in Marion Lake, B. C. , regularly ate neotenic and larval A. gracile. On this basis I conclude that the drop in density of A. gracile in Fay Lake in August, 1975, accompanied by a shift in the population age structure, was due to increased predation by trout dropped into the lake in July.

Alternate explanations for the drop in density may be excluded: a death-dealing catastrophe such as disease would likely affect the different age classes in a similar manner, and would leave dead carcasses lying about. Although I have often seen dead A. gracile in similar lakes in the Cascades, I have seen only one in Fay Lake. Emigration of one year olds through metamorphosis would have been

easily detected, had it occurred, in the regular searches of the lake's shoreline. Finally, movement from the study areas to another area of the lake would have been detected during the regular underwater traversals of the lake. Densities along these traverses fell along with those on the study transects.

So trout eat A. gracile. From the information above, and the destruction of the stationary age distribution in the salamander population, one may infer that trout eat A. gracile enough to act as a key factor (Morris, 1959) affecting the salamander population. In fact, it is quite possible that the trout in Fay Lake act as a keystone predator (Paine, 1966) in the maintenance of the vertebrate community, by keeping the A. gracile population low enough to allow rough-skinned newts (Taricha granulosa) to inhabit the lake. This hypothesis is suggested by the observation that nearby ponds which lack fish also lack newts, and by Neish's (1970) finding that the two salamander species have almost identical diets. The newts are able to inhabit the deeper portions of the lake, since their extremely toxic skin secretions protect them from predation by any vertebrate other than common garter snakes (Thamnophis sirtalis) (Brodie, 1968). A. gracile does not exploit any resource, other than egg-laying sites, deeper than 1.3 m.

Since trout are able to affect Ambystoma populations so drastically, one begins to wonder how A. gracile is able to persist under a regime of introduced predators, while the closely related

A. tigrinum nebulosum in Colorado is not. This answer cannot be elucidated from predator-prey models which produce stability through feedback from prey density to predator population growth rate (Kilmer, 1972; May, 1973), since the stocking of trout (the only source of fish recruitment) is independent of salamander density. Nor can the salamander persistence be derived from a coevolved predator relationship (Pimentel and Al-Aafidh, 1963). Spatial refugia, such that some prey are never exposed to predation because they are inaccessible to the predator, can allow a predator-prey system to persist (Rosenzweig and MacArthur, 1963). However, the habitat selection data give no indication that the salamanders choose to occupy areas which might be inaccessible to fish, such as areas shallower than 15 cm.

Another mechanism permitting persistence of a prey population is immigration. Indeed, regular input of new individuals is the only mechanism with a natural analog which permits laboratory predator-prey systems to persist (e. g. , Salt, 1974). Immigration into the salamander population would involve breeding by terrestrial (metamorphosed) adults, with immigration input appearing as the offspring of such breedings. Such immigration has never been observed: in over 100 hours of searching the shoreline of Fay Lake, I never found a single terrestrial northwestern salamander. I will also note that all egg-deposition in the lake took place while the lake was snowbound by

at least 1 m of snow. Any metamorphosed individuals breeding in the lake would either have to overwinter in the lake, in which case I should have seen them, or they would have to burrow through a meter of snow, and cross solid snow to get to the lake. I cannot believe that terrestrial northwestern salamanders are physiologically capable of either of these behaviors, nor can I accept immigration as a significant population process in Fay Lake.

It is also possible that there is some type of differential size- or age-specific predation on the salamanders, such that large salamanders have a smaller probability of being eaten just because they are too big for many fish to eat. Such a refugium in large size, which would permit persistence of the salamander population, is suggested by the shift in age structure of the salamander population after the drop. It is also obvious the fingerlings of 10-15 cm length cannot eat salamanders of the same size. However there is a sizable reservoir of large (25-90 cm) fish in the lake, which are quite capable of eating any size of salamander. Therefore, while large size alone may reduce the probability of being eaten, it cannot reduce that probability to zero as required to produce a refugium. However, any advantage in predator avoidance inherent in large size could be enhanced to produce a refugium by the repertoire of behaviors exhibited by older, larger salamanders.

The data do indicate that a significant number of salamanders are behaving in a non-random manner that reduces the chances of being eaten by a trout. Indeed, every behavioral attribute quantified in this study can be interpreted as a defense against predation. While some behaviors have other interpretations (e. g. , salamanders may avoid bare mud substrate because few food items are found there), they still serve as a protection against predation. It is evident, then, that part of the mechanism by which the salamander population persists is a behavioral analog of a spatial refuge: there is a reserve of individual salamanders that always avoid predation by fish, no matter what the density of fish. These individuals avoid predation with a set of appropriate behaviors, rather than by occupying an area inaccessible to the predator. The stability of the salamander population can thus be characterized as a stable limit cycle defined by some maximum population size, as exemplified in 1973, and some minimum composed of the core individuals. The actual value of this minimum can vary according to the time-specific reinforcement schedules discussed below.

All of the significant behaviors associated with habitat selection serve a predator avoidance function: for example, the salamanders may avoid shallow water in order to avoid terrestrial predators such as garter snakes (Thamnophis sirtalis and T. ordinoides) which hunt in the shallows, or because seiches and waves there produce sensory

"white noise" which masks the approach of a predatory fish. They may avoid deep water because that is where the fish are most of the time. The slight age-specific differences in preferred depth may be the product of slight differences in age-specific susceptibility to predation. The salamanders may avoid bare mud substrate because they are easily perceived by fish while on it, and because the fish can follow their movement through it should they try to escape into it. When startled they may move from the grass substrate to the mud/grass substrate because the latter is easier to burrow into with speed, and without leaving a trail of disturbed mud.

All of the behaviors described under predator avoidance (orientation, direction of escape, shift, escape movement, and stop position) can only be considered to serve that purpose -- no other explanation obtains.

Aggregation is a well known response to predation (cf. R. J. Taylor, 1976). The advantage stems from the fact that a prey individual minimizes its chances of being eaten when a predator attacks, if another prey individual is nearby to attract the predator first. While northwestern salamanders do not actually flock, they are aggregated to a degree that could produce some confusion in an attacking predator.

Finally, the age-specific social interaction can only be interpreted as a response to predation, but from a predator other than fish:

small salamanders avoid large salamanders in order to avoid being cannibalized. Burger (1950) noted that alternate year classes of larval A. tigrinum nebulosum were wiped out by the cannibalism in the preceding year class. The stationary age distribution of the Fay Lake A. gracile population from 1973 to mid-1975 indicates that no such situation obtains there.

These observed behaviors are not likely to be genetically based (with the possible exception of the age specific interaction). First of all, 25 years or generations is an extremely short period of time in which behavior controlling mutations can arise and spread through the population by natural selection. Secondly, the essentially random behavior of the two year olds, sandwiched between the complexly non-random behaviors of the one and three year olds, indicates that each year class reacts to predation pressure in a different way, depending upon the particular intensity of predation experienced. The three year olds actually include individuals from several generations, some of which probably lived through 1971 and 1972, years of high fish density after the stocking of 1971. (Efford and Mathias (1969) estimated the average life span of neotenic A. gracile at six years.) The two year olds were born in 1973, a year of low fish density when the stocking failed; they were never exposed to high predation pressure while small. The one year olds also were not exposed to high fish density until the drop of 1975. Their non-random behavior prior to the drop

probably reflects their greater vulnerability to predation at any level of predation. (Newly hatched A. gracile are exceedingly feeble swimmers; their prowess at swimming only begins to increase after the emergence of legs in the second or third month of life.) After the drop, their set of behaviors was no longer appropriate, due to the high densities of fingerlings whose predatory behavior was different from that of the larger fish to whom the salamanders were originally accustomed. I therefore surmise that the predator avoidance behaviors are learned, and that the variability in behavior between age classes reflects different learning situations, not ontogenetic release of innate behavior.

A. gracile are capable of learning. That is, they can modify their behavior on the basis of experience. For instance, Henderson (1973) found that larval A. gracile conditioned to eat either benthic or planktonic prey continued to specialize on that prey type when confronted with both types. He also observed specialized feeding on one type or the other in nature, and speculated that such specialization constituted a learned response. Learning of predator avoidance behavior should require only a simple reinforcement schedule: animals choosing a correct response are rewarded with escape from a predator; animals choosing an incorrect response are mauled or killed. The surviving animals, of course, must be aware that they have avoided a noxious experience. This is not hard to accept, given



the fact that some individuals appear to be quite aware of their position within the lake. The number of predator attacks required to reinforce a behavioral sequence is a moot question. That salamanders do survive predator attacks is suggested by the fact that about 5% of the three-year olds were stump-tailed or otherwise disfigured. Such disfigurements occur in less than 1% of the salamanders in Owl Creek, which has no trout predators.

The number of predator attacks an individual might be exposed to while reinforcement occurs must be dependent upon the number of fish present in the lake. Since this must vary according to the degree of success of the stockings, the reinforcement schedules responsible for the avoidance behavior must vary from year to year. Such variation would account for the differences in behavior between the three age classes.

The variation in behavior between age classes enhances the value of each particular set of behaviors, by precluding totally stereotyped behavior upon which a predator can key. Fish are good learners when it comes to getting food (e. g. Ivlev, 1961); some fish even exhibit insight learning capabilities (Lagler, Bardach and Miller, 1962). When confronted by a prey which always reacts in the same manner, the fish should easily learn the most appropriate behavior to counter that of the prey. Variation in behavior between age classes, and within age classes depending upon position in the lake, should produce

a more bewildering array of learning situations for the fish. Such an array might prove to be too complex to be integrated into a cohesive set of counter-behaviors.

There is one final nuance of this study that I should point out, with regard to modelling of predator-prey systems. All such models carry an implicit assumption that all prey individuals are inherently equal in their susceptibility to predation. Even models incorporating a refuge assume that the refuge situation arises from inaccessibility of some individuals only when prey population is low (cf. Rosenzweig and MacArthur, 1963). There are no models incorporating 1) variability in the size of the refuge population, which would occur in the salamander population in Fay Lake with different learning reinforcement schedules; 2) learned behavior as a defense against predators; or 3) individual differences in susceptibility to predation, such that some individuals have a high probability of always avoiding predation, no matter what the predator population density. Until these attributes are included in the predator-prey models, general analysis of predator-prey system stability is futile.

## BIBLIOGRAPHY

- Addicott, John F. 1974. Predation and prey community structure: an experimental study of the effect of Mosquito larvae on the protozoan communities of Pitcher Plants. *Ecology* 55(3):475-492.
- Botkin, Daniel B. and Matthew J. Sobel. 1975. Stability in time-varying ecosystems. *Amer. Nat.* 109:625-646.
- Brodie, E. D. Jr. 1968. Investigations on the skin toxin of the adult rough-skinned newt, Taricha granulosa. *Copeia* 1968:307-313.
- Brooks, J. L. and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150:28-35.
- Burger, W. L. 1950. Novel aspects of the life history of two amphibians. *J. Tenn. Acad. Sci.* 25:252-257.
- Clark, P. J. and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445-453.
- Efford, Ian E. and Jack A. Mathias. 1969. A comparison of two salamander populations in Marion Lake, British Columbia. *Copeia* 1969:723-736.
- Everest, F. H. and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile Chinook salmon and steelhead trout in two Idaho streams. *J. Fish. Res. Bd. Canada* 29:91-100.
- Gause, G. F. 1934. Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science* 79:16-17.
- Gilpin, Michael E. 1973. Do hares eat lynx? *Amer. Nat.* 107:727-730.
- Griffith, J. J. Jr. 1972. Comparative behavior and habitat utilization of brook trout (Salvelinus fontinalis) and cutthroat trout (Salmo clarki) in small streams in northern Idaho. *J. Fish. Res. Bd. Canada* 29:265-273.

- Henderson, Bryan A. 1973. The specialized feeding behavior of Ambystoma gracile in Marion Lake, British Columbia. *Can. Field-Nat.* 87:151-154.
- Holling, C. S. 1961. Principles of insect predation. *Ann. Rev. Entomol.* 6:163-182.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27:343-383.
- International Union for Conservation of Nature and Natural Resources. 1972. Red Data Book, Volume I: Mammalia. Morges, Switzerland, IUCNNR.
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. New Haven, Connecticut, Yale University Press.
- Kilmer, W. L. 1972. On some realistic constraints in prey-predator mathematics. *J. Theor. Biol.* 36:9-22.
- Lagler, Karl F., John E. Bardach and Robert R. Miller. 1962. Ichthyology. New York, John Wiley and Sons.
- Leigh, E. 1968. The ecological role of Volterra's equations. in M. Gerstenhaber, ed. Some mathematical problems in biology. Providence, Rhode Island, American Mathematical Society.
- Licht, Lawrence E. 1975. Growth and food of larval Ambystoma gracile from a lowland population in southwestern British Columbia. *Can. J. Zool.* 53:1716-1722.
- Luckinbill, Leo S. 1973. Coexistence in laboratory populations of Paramecium aurelia and its predator Didinium nasutum. *Ecology* 54:1320-1327.
- \_\_\_\_\_. 1974. The effects of space and enrichment on a predator-prey system. *Ecology* 55:1142-1147.
- MacArthur, Robert H. 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology* 36:353-356.
- MacLulich, D. A. 1937. Fluctuations in the number of the varying hare (Lepus americanus). U. of Toronto Studies, Biological Series number 43.

- Maly, Edward J. 1969. A laboratory study of the interaction between the predatory rotifer Asplanchna and Paramecium. Ecology 50:59-73.
- May, Robert M. 1973. Stability and complexity in model ecosystems. Princeton, New Jersey, Princeton University Press.
- Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. 1. Structure and prediction. Aust. J. Zool. 1:163-173.
- Morris, R. F. 1959. Single factor analysis in population dynamics. Ecology 45:119-131.
- Neish, I. C. 1970. A comparative analysis of the feeding behavior of two salamander populations in Marion Lake, B. C. Unpublished Ph. D. thesis, U. of British Columbia, Vancouver.
- \_\_\_\_\_. 1971. Comparison of size, structure and distributional patterns of two salamander populations in Marion Lake, British Columbia. J. Fish. Res. Bd. Canada 28:49-58.
- Noble, G. Kingsley. 1931. The biology of the amphibia. New York, Dover Press.
- Paine, R. T. 1966. Food web complexity and species diversity. Amer. Nat. 100:65-75.
- Pimentel, O. and R. Al-Aafidh. 1963. The coexistence of insect parasites and hosts in laboratory populations. Ann. Entomol. Soc. Amer. 56:676-678.
- Rosenzweig, M. L. and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. Amer. Nat. 97:209-223.
- Salt, George W. 1974. Predator and prey densities as controls of the rate of capture by the predator Didinium nasutum. Ecology 55:434-439.
- Snyder, Richard C. 1956. Comparative features of the life histories of Ambystoma gracile (Baird) from populations at low and high altitudes. Copeia 1956:41-50.
- \_\_\_\_\_. 1963. Ambystoma gracile. Cat. Amer. Amphib. Rept. 6. 1-6. 2.

- Sprules, W. Gary. 1974. The adaptive significance of paedogenesis in North American species of Ambystoma (Amphibia: Caudata): an hypothesis. *Can. J. Zool.* 52:393-400.
- Taylor, Robert J. 1976. Value of clumping to prey and the evolutionary response of ambush predators. *Amer. Nat.* 110:13-29.
- Watt, K. E. F. 1959. A mathematical model for the effect of densities of attacked and attacking species on the number attacked. *Canad. Ent.* 91:129-144.