

ACTIVITY PATTERNS AND
ESCAPE BEHAVIOR OF THE
SLENDER SALAMANDER
(Batrachoseps attenuatus)

by

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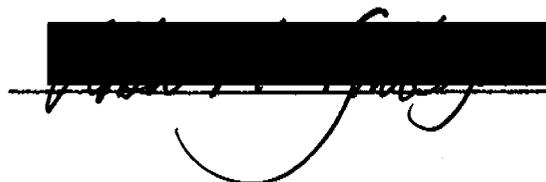


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ABSTRACT

Seasonal surface activity patterns and predator escape behavior of the California slender salamander (Batrachoseps attenuatus) were studied from March through August 1971, near Crannell, California. The habitat types investigated included: 1) second growth coast redwood (Sequoia sempervirens) forest, 2) grassland and 3) the forest/grassland edge.

Surface activity was positively correlated with rainfall and ground temperatures. From March through August the monthly mean number of animals found during the diurnal sample decreased by 50.0 percent in grassland habitats. Nocturnal surface activity remained relatively constant in all habitats from March through August. Limited data suggest that this species becomes nocturnal during the drier summer months. With relative humidity greater than 70 percent, this species' temperature preference ranges from 10° to 15.5° C. From March through August 61.9 percent of the animals collected in the field were found within this temperature range. During this same period, the monthly percentage of animals with absent or regenerating tails increased from 24.3 to 45.2 in the redwood forest, 26.9 to 73.9 in the edge and 28.9 to 73.9 in the grassland habitats.

Slender salamanders exhibited protean displays when presented with tactile and olfactory stimuli. Protean behavior is defined as that behavior which is sufficiently unsystematic to prevent a predator from predicting in detail the position or actions of the prey. Direction of movement of the protean display from a consistent tactile stimulus contact point appeared to be random. The mean distance and time of movement were 11.5 cm and 1.02 s respectively.

Chemical extracts of potential predators elicited protean responses only in slender salamanders with regenerating tails. Animals with regenerating tails exhibited protean displays when exposed to chemical extracts of these species: Pacific giant salamander (Dicamptodon ensatus), arboreal salamander (Aneides lugubris), ringneck snake (Diadophis punctatus), common garter snake (Thamnophis sirtalis), western terrestrial garter snake (T. elegans) and western aquatic garter snake (T. couchi). Exposure to the chemical extracts of these species followed by a tactile stimulus resulted in a 22.5 ± 9.3 percent increase in the mean distance moved during the protean display. No difference was noted in the distance moved by animals with regenerating or complete tails.

Predator-prey interactions of 22 potential vertebrate predators and slender salamanders indicated the following: 1) variable prey palatability but no lethal effects when prey was ingested, 2) successful attacks on salamanders were made to the head and body area, 3) unsuccessful attacks were made on the tail, 4) the protean display was observed in 10.0 percent of successful attacks and 79.2 percent of unsuccessful attacks, and 5) tail autotomy occurred in 0.01 percent of successful attacks and 63.2 percent of unsuccessful attacks.

The protean display delayed the predator's reaction time and thereby reduced the effectiveness of the predatory response. The protean display probably insures against learned counter measures by incorporating unpredictability as a basic behavior component. Prey which employ behavior patterns unfamiliar to the predator will be at a selective advantage.

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I. INTRODUCTION

This study of the California slender salamander (Batrachoseps attenuatus) was conducted from March 1 to August 30, 1971, near Crannell, California, in northwestern Humboldt County.

This small plethodontid (lungless) salamander occurs in the coast ranges of southwestern Oregon and California south to the Santa Ana Mountains. Inland it is found on the southern slope of the Transverse Mountains and the western foothills of the central Sierra Nevada (Stebbins 1972:60). Within this range, it is a widespread and abundant species which occurs in a variety of habitats from redwood (Sequoia sempervirens) forest and oak (Quercus spp.) woodlands to yards and vacant lots in the cities. Rainfall, temperature, fog and the patterns of seasonal variations of these climatic factors vary considerably over its range. The annual distribution of rainfall within the range results in seasonal surface activity pattern of this salamander, since it requires a moist microclimate for respiration through its skin. The slender salamander is a predator of the soil macrofauna and feeding is largely confined to the wet season (Maiorana 1971). In the drier parts of the range it retreats underground in summer when it utilizes fat stored in the tail (Hendrickson 1954, Maiorana 1974).

Stebbins (1954) summarized available information on the habitat, reproduction and behavior of slender salamanders. No quantitative study of its behavior or life history was then available. Hendrickson (1954) provided the first study which yielded information on density, home range size, surface activity with respect to rainfall and ground

temperature, rates of growth and tail regeneration. Anderson (1960) studied a number of ecological characteristics of mainland and island populations of California slender salamanders. Cunningham (1960) studied the Pacific slender salamander (B. major), a congeneric species with similar ecological requirements to that of the California slender salamander, and provided information on surface activity relative to temperature and moisture, home range size and movement patterns with respect to cover and moisture. Maiorana (1971) examined aspects of the feeding behavior of the California slender salamander with respect to the seasonal and habitat variation in the amount and type of prey in the diet and of variations in diet with body size. Maiorana (1974) also conducted a study of the behavioral ecology of the California slender salamander which provided information on energy limitation and its effects on body size, the role of tail length in reproduction and predation, and surface activity related to climatic fluctuations analyzed with respect to food availability.

Several workers (Hendrickson 1954, Anderson 1960, Cunningham 1960) have shown the relationships of climatic factors and surface activity. However, these studies were conducted in areas where lack of rainfall and increased ground temperatures eliminate summer surface activity. Therefore, this study of surface activity at the cool-moist extremity of the species distribution and the concomitant increased exposure to predation will be useful for the analysis of predator escape behavior and its ecological implications.

Stebbins (1954:63) first described the predator defense behavior of the California slender salamander as follows: "They may assume a watch-spring-like coil when at rest.

When molested, they commonly engage in violent and random lateral undulations of the body, which usually result in their bodies being thrown in the air. The tail may be shed, but is without a fixed breaking point." The difficulty of handling this species because of this response has been documented by many workers (Hendrickson 1954, Anderson 1960, Cunningham 1960, Maiorana 1971,1974). Stebbins (1972:59) was also the first to ascribe a predator defense or survival value to this behavior by indicating that if the tail was seized, it may snap off and thrash about while the salamander crawls beneath a nearby object and "freezes". He suggested that the thrashing tail may divert the attention of predators.

The fundamental ecological principles and the general strategies recognized in predator defense have come from the analyses of numerous individual predator-prey interactions. Well known examples among salamanders include the evolution of mimicry (Brodie and Howard 1972), the principles of camouflage or cryptic coloration, Smyth (1962), and biochemical defenses (Webster 1960, Brodie 1968a,1968b, Brodie and Gidson 1969). Biochemical defenses in the form of mucous or granular glands are present in the majority of salamander species. Mucous glands are distributed over the entire body and secrete a watery to viscous mucus which keeps the skin moist in terrestrial situations. In newts this mucus secretion is toxic and provides protection from predators. Granular or venom glands are usually concentrated in strategic areas such as the parotoid glands or along the mid-dorsal line from the nape of the neck to the tip of the tail. These glands secrete an alkaloidlike substance which resembles digitalis in action. These venoms may be sufficiently potent to kill large vertebrates by increasing tonicity of the heart, weakening respiration and causing general muscular paralysis and nausea (Noble 1931, Francis 1934, Bernstein 1953, Porter 1972).

A review of the literature dealing with skin gland secretion has not yielded any work on this subject in the genus Batrachoseps. Esterly (1904) described dilator and constrictor muscles about the mouths of venom glands in the closely related genus, Plethodon. He stated that the method of secretion was a continuous flow. The evolution in B. attenuatus of an elaborate predator escape behavior would suggest the ineffectiveness of skin gland secretions alone in providing adequate defense against potential predators.

The theoretical possibility that irregular behavior might serve as a defense against predators was offered by Chance and Russell (1959) and the existence of "protean displays" has been confirmed by Humphries and Driver (1967, 1970). Protean behavior is defined as that behavior which is sufficiently unsystematic to prevent a predator predicting in detail the position or actions of the prey. Much of this paper is concerned with various forms of protean behavior exhibited by California slender salamanders and the ecological implications in the evolution of this predator-prey interaction.

The relationship between a predator and its prey is a fundamental aspect of animal ecology. Behavioral mechanisms are fundamental to both competitive and predatory interactions (Klopfer 1962, Miller 1967) and yet the experimental study of such behavioral mechanisms is still quite primitive. Most studies have centered on the end result of this relationship -- its effect on population dynamics and trophic structure within the community. The analysis of the processes involved in predator-prey interactions has been dealt with by the ethologist rather than ecologist (Tinbergen et al. 1967, Beukema 1968, Edmunds 1974).

The objectives of the study were as follows: 1) evaluate

surface activity patterns with respect to climatic variations in rainfall, ground temperature and fog in 3 habitat types occurring in the wettest portions of this species' range, and 2) quantify the types of escape responses exhibited by this species when confronted by potential vertebrate predators under controlled conditions.

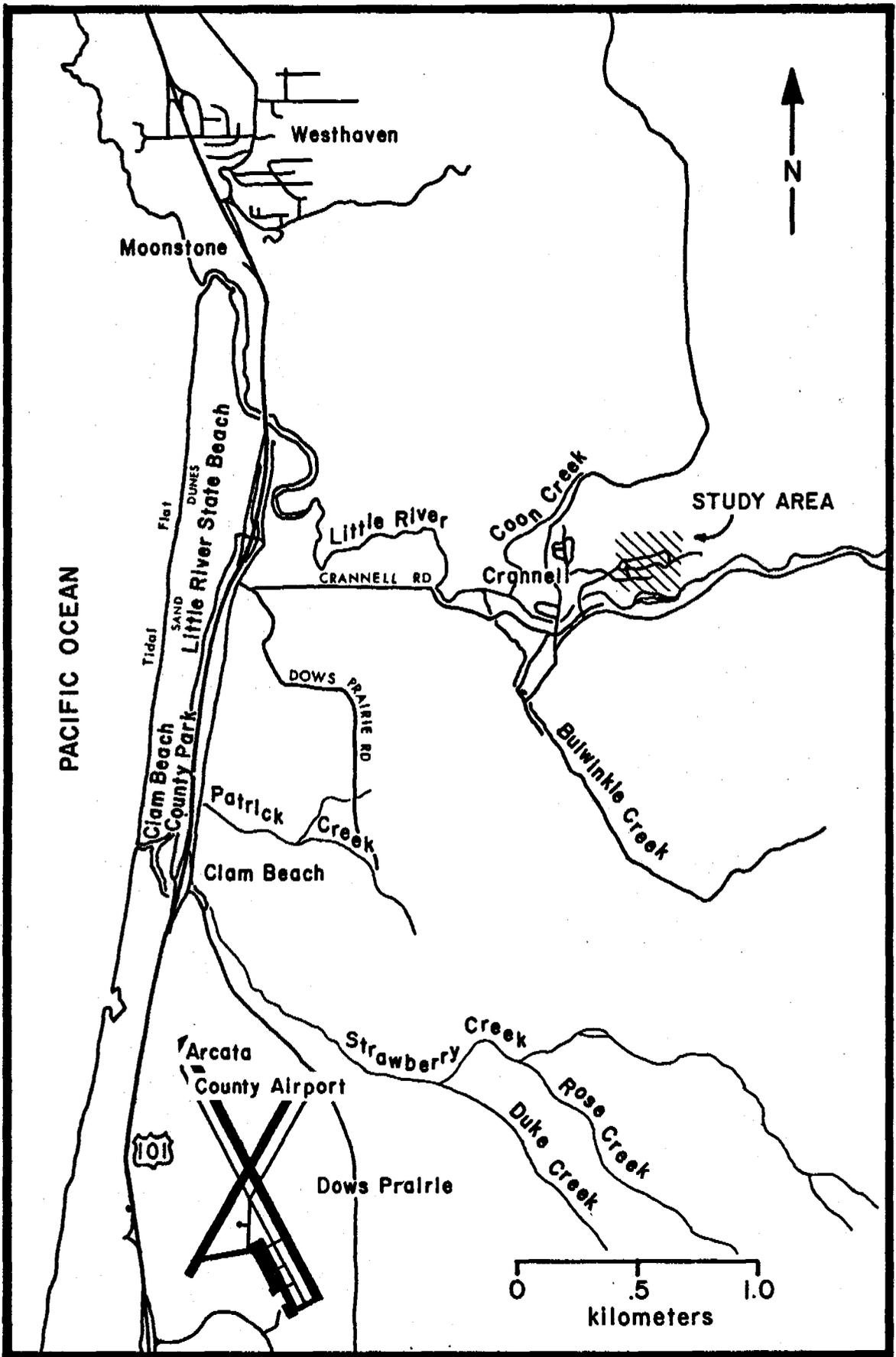
To meet these objectives, a series of studies were initiated which would attempt to indicate the relationship between seasonal surface activity patterns and protean defense behavior. Surface activity was quantified by systematically sampling areas within 3 habitat types and daily recording these climatic variables: rainfall, ground temperature and fog. Protean defense behavior was examined in a series of laboratory experiments which tested slender salamanders taken from these 3 habitats during March, June and August. Slender salamanders were tested to determine the nature of the protean response to tactile, visual and olfactory stimuli. The palatability and defense behavior of these salamanders to potential vertebrate predators was also tested to determine if correlations existed between the protean display eliciting mechanism, prey palatability and defense behavior.

II. STUDY AREA

The study area lies within the coastal redwood region which extends from Brookings, Oregon, on the north to central Monterey County on the south (Waring and Major 1964). Little River which empties into the Pacific Ocean just north of Clam Beach County Park in Humboldt County exerts considerable influence on the stream side vegetation through periodic flooding (U.S. Geologic Survey 1971), (Figure 1). This small river valley acts as a pathway for the inland movement of fog from the Pacific Ocean, 2.0 km to the west. The fog zone has been closely correlated with the distribution of the coast redwood (Waring and Major 1964). The study area was dominated by a stand of second growth coast redwood which occurred on a gentle south facing slope with elevations ranging from 12 to 110 m. The site, like most of coastal California, is characterized by dry cool summers and cool rainy winters. The Pacific Ocean and coastal fog have a moderating influence and the annual range of average temperatures is not as great as it is further inland. The U.S. Weather Bureau recording station located 3.0 km southwest of the study area at the McKinleyville-Arcata-Eureka airport provided 10 year (1951-1960) climatological data for the region (U.S. Weather Bureau 1960). Winter mean maximum and minimum temperatures were 11.7° to 5.0° C. Summer mean maximum and minimum temperatures were 16.1° to 10.6° C. The mean temperatures for January and July were 8.3° and 13.9° respectively and the mean annual temperature was 11.1° C.

Due to the proximity of the Pacific Ocean the study area is subject to frequent and severe winter rainstorms from October through May. Average annual precipitation was about

Figure 1. Location of the study area, Crannell, California.

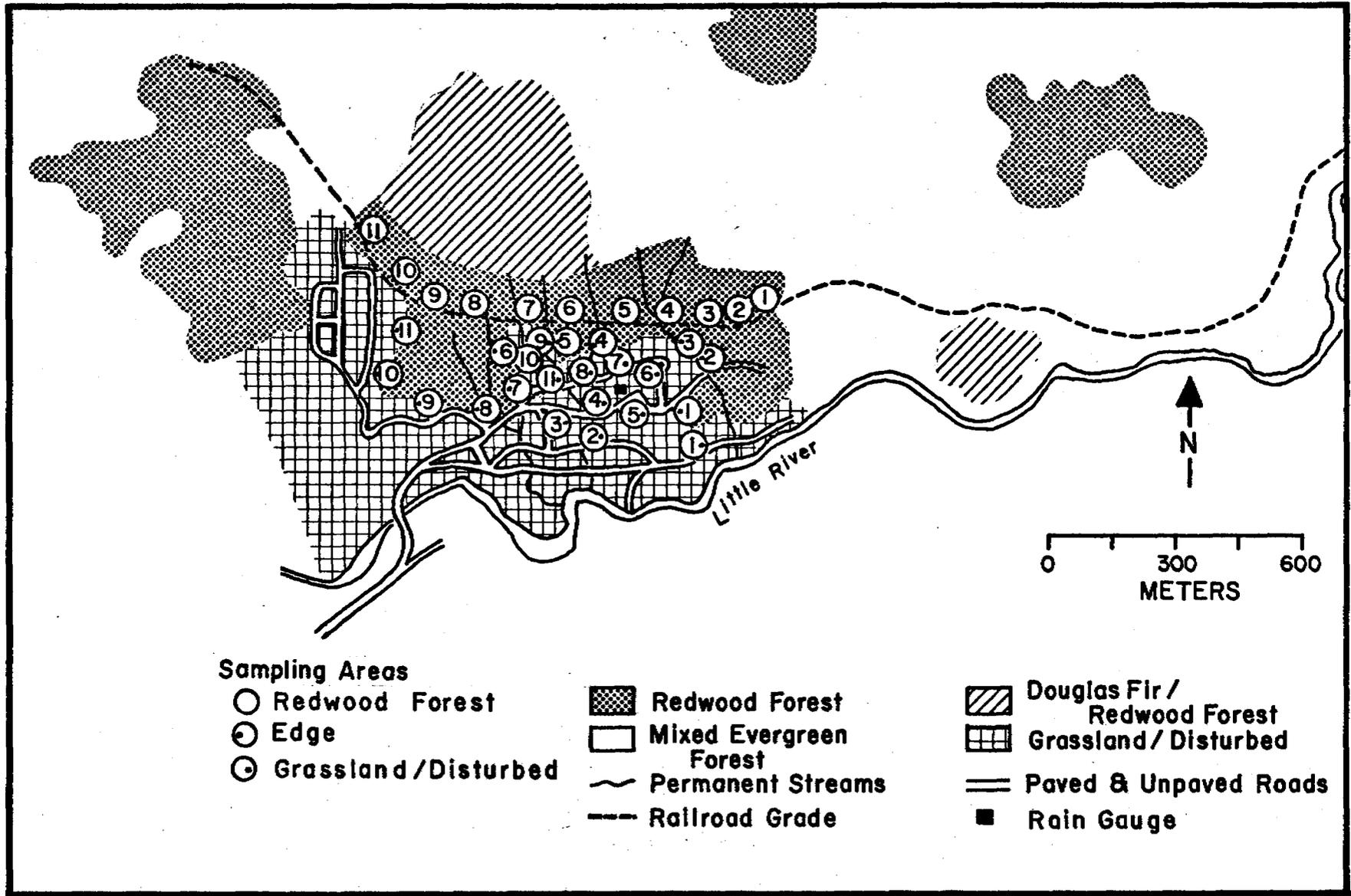


100 cm. Winter mean monthly maximum precipitation ranged from 16.5 to 17.8 cm. Summer mean monthly maximum precipitation was 0.3 cm. Low dense fog frequently occurs in this area throughout the year. Winter fog usually precedes and follows periods of rainfall. When present, summer fog usually remains until midday and returns by early evening. The prevailing climatic conditions of heavy winter rainfall and frequent summer fog combined with the existing soil characteristics of the area have provided an excellent growing site for redwood coniferous forest (Waring and Major 1964).

No logging had occurred in the study area since the late 1800's. An abandoned railroad bed, numerous logging skid trails and unpaved roads occur throughout the area. The residential structures in the town of Crannell were razed in 1969 by the property owners, the Georgia-Pacific Lumber Company. The abandonment of the town had resulted in considerable debris and downed lumber being strewn about the area. These objects significantly increased the amount of available cover for amphibians and reptiles within the study area.

About 35 percent of the study area was dominated by a second growth stand of redwood which gradually intergraded into mixed evergreen forest at the 122 m elevation contour (Figure 2). The northern limit of this redwood stand graded into a coniferous forest type dominated by Douglas fir (Pseudotsuga menziesii) with redwood present as a subdominant species. When first developed, the town site was cleared of most native trees and many horticultural species of trees and shrubs were later introduced. The town site area was open and the dominant ground cover consisted of annual and perennial grasses, horticultural shrubs, vines and flowers. Therefore, this habitat type has been termed grassland/disturbed.

Figure 2. Location of the sampling areas within the redwood forest, the edge and the grassland/disturbed habitats of the study area.



The edge habitat existing between the redwood forest and grassland/disturbed habitat was a composite of both types. Although the boundaries of this habitat type cannot be accurately delineated, it occupied approximately a 30 m strip at the forest/grassland interface.

Several small perennial creeks traverse the study area. These creeks were bordered by sedges (Carex spp.), wiregrass (Juncus spp.), horsetail (Equisetum sp.) and perennial grasses. Table 1 is a partial listing of the dominant plant species found within the redwood forest, the edge and the grassland/disturbed habitats of the study area.

Eleven sampling areas were located within each of the 3 habitat types selected for study. Each sampling area encompassed about 10 m² (Figure 2, Table 2).

Table 1. A partial list of the dominant plants found within the redwood forest, the edge and the grassland/disturbed habitats of the study area.

Plant Species	Scientific Name	Habitat Types		
		Redwood Forest	Grassland/ Disturbed	Edge
Trees:				
Redwood	<u>Sequoia sempervirens</u>	x		x
Douglas fir	<u>Pseudotsuga menziesii</u>	x		x
California bay	<u>Umbellularia californica</u>	x		x
Tanoak	<u>Lithocarpus densiflorus</u>			x
Red alder	<u>Alnus rubra</u>			x
Western red cedar	<u>Thuja plicata</u>		x	
Shrubs:				
Rhododendron	<u>Rhododendron occidentaleis</u>	x		x
Wood rose	<u>Rosa gymnocarpa</u>	x		
Thimble-berry	<u>Rubus parviflorus</u>	x		x
Himalaya berry	<u>R. procerus</u>		x	x
Canyon gooseberry	<u>Ribes menziesii</u>	x		x
Blue blossom	<u>Ceanothus thyrsiflorus</u>		x	x
Black huckleberry	<u>Vaccinium ovatum</u>			
Red huckleberry	<u>V. parvifolium</u>			
Salal	<u>Gaultheria shallon</u>	x		x
Oregon grape	<u>Berberis nervosa</u>	x		x
Coyote bush	<u>Baccharis pilularis</u> var. <u>consanguinea</u>		x	x
Fire-thorn	<u>Pyracantha coccinea</u>		x	
Cotoneaster	<u>Cotoneaster dwaricata</u>		x	
Fuschia	<u>Fuschia</u> spp.		x	

Source: (Munz and Keck 1959)

Forbs and Herbs:

Horse tail	<u>Equisetum</u> spp.	x	x	x
Redwood sorrel	<u>Oxalis oregana</u>	x		x
Redwood violet	<u>Viola sempervirens</u>	x		x
Fairy lantern	<u>Disporum smithii</u>	x		
Common trillium	<u>Trillium sessile</u>	x		
Trillium	<u>T. ovatum</u>	x		x
Brook trillium	<u>T. rivale</u>	x		
Ginger	<u>Asarum caudatum</u>	x		
Oregon lily	<u>Lilium columbianum</u>	x		x
Fetid adders' tongue	<u>Scoliopus bigelovii</u>	x		
Clintonia	<u>Clintonia andrewsiana</u>	x		x
Oregon coltsfoot	<u>Maianthemum dilatatum</u>	x		x
Foxglove	<u>Digitalis purpurea</u>			x
Sword fern	<u>Polystichum munitum</u>	x	x	x
Lady fern	<u>Athyrium filex-femina</u>	x		x
Curley dock	<u>Rumex crispus</u>		x	
California buttercup	<u>Ranunculus californicus</u>		x	x
Dandelion	<u>Taraxacum vulgare</u>		x	x
Mint	<u>Mentha</u> sp.		x	
English daisy	<u>Bellis perennis</u>		x	x

Grasses:

Brome grass	<u>Bromus</u> spp.		x	x
Fescue grass	<u>Festuca</u> spp.		x	x
Blue grass	<u>Poa</u> sp.			x
Quaking grass	<u>Briza minor</u>		x	
Wild barley	<u>Hordeum</u> spp.		x	x
Italian rye grass	<u>Lolium multiflorum</u>		x	x
Wild oat	<u>Avena fatua</u>		x	x
Spear grass	<u>Stipa</u> sp.	x	x	x
Sedge	<u>Carex</u> spp.	x	x	x
Rush	<u>Juncus</u> sp.	x	x	x

Table 2. A summary of the habitat characteristics associated with each sampling area located within the redwood forest, the edge and the grassland/disturbed habitats within the study area.

Sampling Area No.	Habitat Type	Associated Understory Plants	Mean Light Intensity* (foot candles)	Cover Object Type and No.		Total Cover Object Area cm ²	Ground Cover Type	
				Downed Limbs	Milled Lumber		Under Cover Object	Adjacent to Cover Object
1	Redwood Forest	red alder	30/20	10	0	3999	redwood leaf litter	redwood leaf litter
2	Redwood Forest	red alder	18/12	2	0	1967	redwood leaf litter	redwood leaf litter
3	Redwood Forest	sorrel	25/16	3	0	1593	redwood leaf litter	redwood leaf litter
4	Redwood Forest	sorrel	20/17	2	0	774	redwood leaf litter	redwood leaf litter
5	Redwood Forest	sorrel	19/12	1	0	2089	soil	redwood leaf litter
6	Redwood Forest	blackberry, red alder, rhododendron	20/14	1	0	1471	redwood leaf litter	redwood leaf litter
7	Redwood Forest	sorrel	1./10	3	0	3134	soil	redwood leaf litter
8	Redwood Forest	sorrel, sword fern	24/18	1	0	2064	soil	redwood leaf litter
9	Redwood Forest	sorrel, sword fern	20/16	0	2	2580	redwood leaf litter	redwood leaf litter
10	Redwood Forest	sorrel, sword fern	30/20	0	2	1644	redwood leaf litter	redwood leaf litter
11	Redwood Forest	sorrel	18/14	0	4	2341	redwood leaf litter	redwood leaf litter
1	Edge	red alder, thimble-berry, grass	65/40	3	0	1728	grass	grass
2	Edge	red alder, coyote bush, grass	80/65	0	3	2167	soil	grass
3	Edge	red alder, coyote bush, thimble-berry, grass	48/32	0	1	2245	soil	grass
4	Edge	thimble-berry	95/65	0	3	2967	redwood leaf litter	redwood leaf litter
5	Edge	coyote bush	90/60	1	2	2064	soil	redwood leaf litter
6	Edge	red alder, thimble-berry, grass	80/63	1	3	2515	soil	grass
7	Edge	red alder, coyote bush	42/30	1	2	2967	soil	grass
8	Edge	thimble-berry	72/65	2	3	3418	soil	grass
9	Edge	coyote bush	110/80	3	1	2612	soil	grass

10	Edge	pyracantha	126/100	1	2	1741	grass	grass
11	Edge	red alder, thimble-berry	160/120	3	0	2709	redwood leaf litter	redwood leaf litter
1	Grassland/ Disturbed	pyracantha	850/400	0	1	1728	soil	grass
2	Grassland/ Disturbed	grass	900/425	0	3	2096	grass	grass
3	Grassland/ Disturbed	grass, horsetail, foxglove	925/450	0	3	1393	soil	grass
4	Grassland/ Disturbed	grass, horsetail, plantain	900/325	0	1	2902	soil	grass
5	Grassland/ Disturbed	grass, sedge, dock	700/250	0	1	13,467	grass	grass
6	Grassland/ Disturbed	grass, sedge, dock	600/220	0	2	4586	soil	grass
7	Grassland/ Disturbed	grass, sedge, dock	700/270	0	3	2864	soil	grass
8	Grassland/ Disturbed	horsetail, grass	800/300	0	1	929	soil	grass
9	Grassland/ Disturbed	horsetail, grass, dock, mint	700/280	0	2	4412	soil	grass
10	Grassland/ Disturbed	grass	900/325	0	3	4528	soil	grass
11	Grassland/ Disturbed	grass	950/350	0	4	3677	soil	grass

* Mean light intensity expressed as the amount of light (fc) reflected at 30.5 cm from the ground. Numerator equals full sun measurement; denominator equals overcast measurement. Refer to III. Methods, Surface Activity, for details regarding this measurement.

III. METHODS AND MATERIALS

Surface Activity Patterns

Eleven sampling areas were subjectively located in each of these habitat types: redwood forest, edge and grassland/disturbed. Areas were selected which contained 1 to 10 existing ground cover objects. Sampling areas were located within several minutes walking distance of one another to reduce the time required to complete each sample.

To record variations in climatic factors which may effect slender salamanders, a non-recording U.S. Weather Bureau rain gauge was located in the center of the study area (Figure 2). Rainfall measurements and morning, afternoon and evening fog conditions were recorded daily from March through June 1971. Daily rainfall measurements and fog conditions for July and August 1971 were also obtained from the records of the U.S. Weather Bureau recording station located at the McKinleyville-Arcata-Eureka Airport (MAEA), (Figure 1). Comparison of rainfall and fog data for March through June 1971 indicated no significant differences between the study area and the MAEA. In addition, the small amount of rainfall recorded for July and August would minimize any potential differences.

From March through June 1971, ground temperatures under cover objects were recorded every 4 days at 1500 and 2100 hours. Temperature measurements were taken at sampling areas 1, 3 and 9 in the redwood forest type, 3, 7 and 9 in edge and 5, 7 and 11 in grassland/disturbed habitats. During July and August 1971, ground temperatures were obtained from recording thermographs located at sampling area 3 in redwood forest, area 7 in edge and area 7 in grassland/disturbed. For each sampling area a galvanized wash tub was sunk in the

earth until the rim was almost flush with the surface. The thermograph was placed in the tub and covered with a plastic sheet. The recording element was placed under the nearest characteristic cover object. The cover object was held in place by 25-cm wooden stakes. Every effort was made to select a cover object that was similar in character and exposure to others within the same habitat type. During July and August, ground temperature variations between the chosen cover object and other cover objects was $\pm 0.5^{\circ}$ C.

To determine variations in canopy cover density, the mean light intensity at each sampling area was measured using a technique developed at the Virginia Cooperative Wildlife Research Unit (deVos and Mosby 1963:58). The instruments used were 2 Weston Master V light meters, Model 748, supported in a wooden frame 20.3 cm above a 20.3 cm square board painted with white aluminum paint. The light reading was taken with the photoelectric cell pointing downward; therefore the reading was obtained from the light reflected from the base of the frame. The photoelectric meters were set at a film speed of 100 ASA and a shutter speed of 1/125 of a second. One of the 2 instruments was placed on the ground under the cover to be measured and the other was placed in full sunlight. At a given signal both instruments were read and the f-stop measurement recorded. Five measurements were taken at each sampling area under full sunlight and overcast conditions. All measurements were taken at midday when the sun was at its highest point. The disadvantage of this system was that the measurement was expressed as a ratio between full and partial light and not as an absolute light intensity value.

Another system was adopted after the study was completed to allow conversion of these measurements to absolute light intensity values expressed in foot candles (fc). A Sekonic Illuminator, Model 246, reading directly in foot candles was

used to obtain reflected light intensity values. This photoelectric meter was held 30.5 cm above the natural ground cover and a measurement was recorded. The measurement indicated the amount of light in foot candles reflected from the natural ground cover at 30.5 cm above the ground. A measurement was then immediately taken using the previously described apparatus. Forty measurements were taken in full sun and overcast conditions in forest, edge and grassland/disturbed habitats with both instruments until a conversion table could be prepared. From this conversion table all ratio canopy cover measurements were converted to the reflected light intensity measurements (fc) presented here. This conversion table was compared with one prepared by Ray (1975) and no apparent differences were noted.

Sampling Technique

The 33 sampling areas were visited every 4 days at about 1500 hours and 2100 hours from March through June 1971. The areas were visited every 14 days at these same times in July and August. Weather conditions were noted and the rainfall measurement taken. Ground temperatures under cover objects were recorded with a quick recording mercury thermometer for sampling areas 1, 3 and 9 in redwood forest, 3, 7 and 9 in edge and 5, 7 and 11 in grassland/disturbed habitat. Since ground measurements varied $\pm 0.5^{\circ}$ C within each habitat type, measurements at every sampling area were not felt to be necessary. Downed limbs and branches and milled lumber were permanently identified with numbered plastic tags. During each sampling all cover objects were turned and the immediate adjacent ground cover searched for animals. To facilitate capturing more animals, many workers (Hendrickson 1954, Anderson 1960, Cunningham 1960) have added additional cover objects to the study area. No additional cover objects were

added to each sampling area since it was felt that increasing cover would alter surface activity patterns.

When captured, an animal was individually marked by toe clipping. The toe clipping technique used was described by Hendrickson (1954) and Cunningham (1960). Three toes on each foot were sufficiently discernable from the general foot mass to be used in the marking. A different combination of toes was removed from each animal. The inner toe on each foot, because of its small size, was not used. Within the 6 month study period, significant regeneration of clipped toes was not observed. Since 2 to 6 toes were clipped in marking an animal, regeneration of all toes was rather unlikely and would indicate that few, if any, animals were erroneously remarked. Toe clipping was done with the aid of a 20X hand lens. Toe removal was done with an X-ACTO knife fitted with a No. 4 blade. The cutting surface used was a white lucite plastic block, measuring 10 cm x 5 cm x 1 cm. To increase regeneration time, about one half of the toe was removed.

When first captured, the approximate location of each animal was indicated on the cover object with a plastic tag. If the animal was a recapture, the distance from the original capture site was recorded.

The snout vent length (SVL) measurement of each animal first collected was recorded to the nearest millimeter. However, this standard measurement proved to be unsatisfactory for a small salamander with a powerful righting action. Problems associated with measuring animals particularly during the evening sample were acute. A technique used by Hendrickson (1954), Anderson (1960) and Cunningham (1960) was adopted for this study. Animals were measured from the tip of the nose to the anterior surface of the hind limb, that limb being held perpendicular to the body. This measurement could be made on unrestrained animals without rough handling and risk of injury. To convert this body measurement

to a snout vent measurement, 40 live animals were anesthetized and measured using both measurements. From these measurements a conversion table was constructed by means of which all body measurements were converted to the snout vent measurements presented here.

The tail condition of each animal was recorded as normal, absent or regenerating. A normal tail had no irregularities and did not show evidence of a recent break or significant change in pigmentation. Absent tails were those showing a recent breaking point that had not started to regenerate. Regenerating tails had significant changes in pigmentation and had not yet formed the complete, slender fusiform shape.

Notations were made regarding any behavioral characteristics, particularly the protean display. In addition, the watch-spring coil that this species sometimes assumes when at rest was also noted.

Temperature Preference

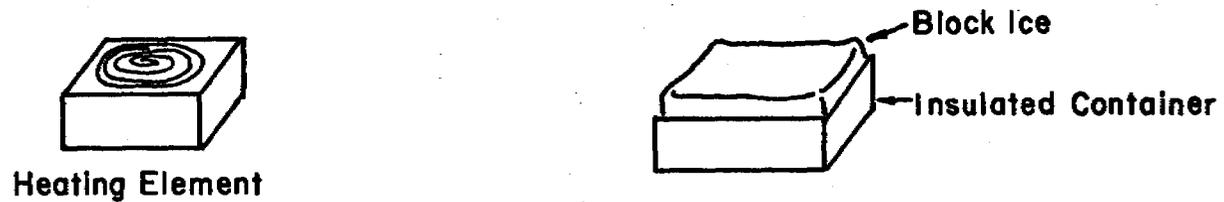
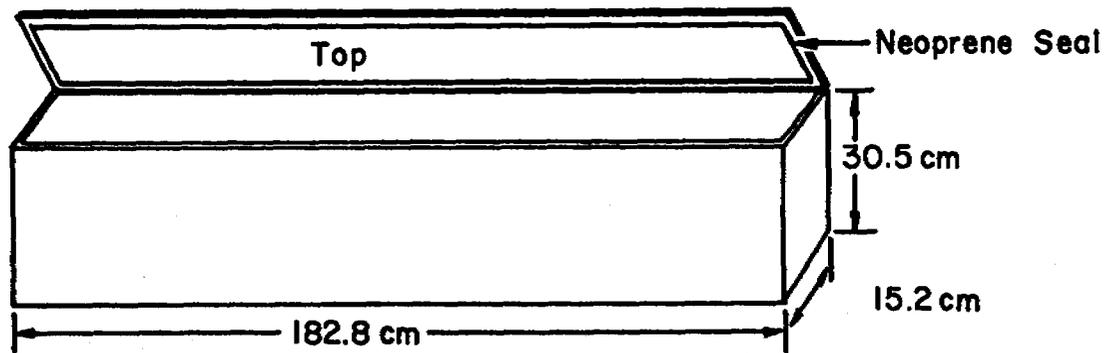
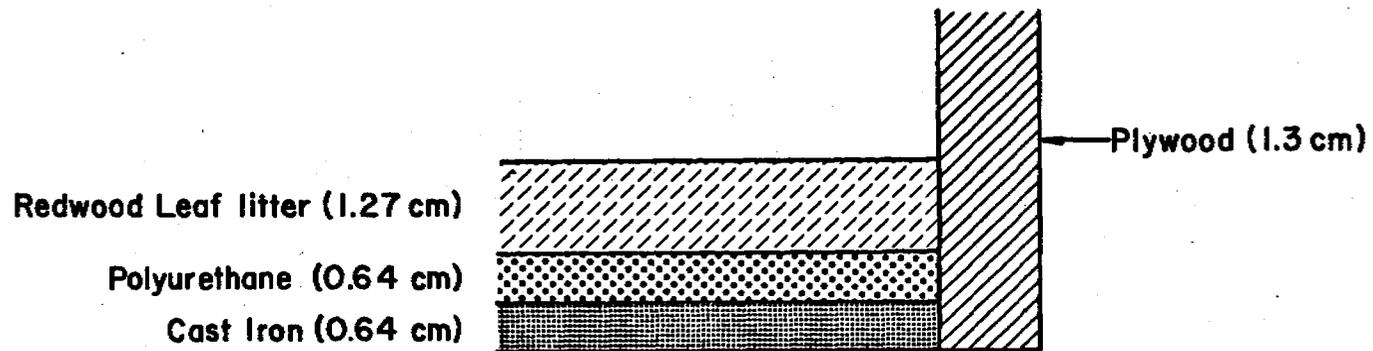
Temperature preference studies were conducted using groups of 100 adult slender salamanders (SVL > 33 mm) collected from the redwood forest, edge and grassland/disturbed habitats within the study area. Animals were collected and tested in April, June and August 1971. Animals were collected from within the study area, but not from within the individual sampling areas. Adult salamanders were exclusively used in this and subsequent experiments because sufficient numbers of juvenile salamanders (SVL < 33 mm) could not be collected to provide a test group of 100 individuals. The age/size class categories of adult (SVL > 33 mm) and juvenile (SVL < 33 mm) were based upon analysis of SVL frequency distribution histograms prepared from 150 animals collected in March and April in redwood forest, edge and grassland/disturbed habitats. The resulting age/size class categories were

similar to those described for slender salamanders collected in Humboldt County by Hendrickson (1954).

All slender salamanders collected in this study were maintained in 3.8 L glass jars filled with redwood leaf litter and moss. About 0.1 L of water was added daily to the jars to maintain a relative humidity of 70 percent or greater. A 70 percent or greater relative humidity level avoids heat and respiratory stress (Czopek 1962, Whiteford and Hutchinson 1965, Cunningham 1966). Hendrickson (1954), Cunningham (1960) and Maiorana (1974) also suggested a 70 percent or greater relative humidity level to maintain captive salamanders. The glass jars were kept in insulated styrofoam containers and maintained at temperatures between 10 to 15° C. The salamanders were fed weekly with fruit flies (Drosophila sp.).

The temperature preference of slender salamanders was tested by placing the animals in a wide thermal gradient with a relative humidity of 70 percent or greater. The technique used was modified from that described by Whiteford and Massey (1970). The test apparatus consisted of a plywood box measuring 15.2 cm x 30.5 cm x 182.8 cm fitted with a 0.64 cm thick cast iron metal bottom and 1.3 cm thick plywood cover (Figure 3). Cast iron was selected over other materials due to its excellent temperature conduction and retention properties. The cover was fitted with a neoprene seal to maintain constant temperature and relative humidity. To provide a water retaining material, the inside bottom was fitted with a 0.64 cm layer of polyethylene foam. A 1.27 cm layer of redwood leaf litter was placed on the foam to provide natural ground cover. A thermostatically controlled 110 volt hot plate was used as the heating element. A piece of block ice, measuring about 30.5 cm x 30.5 cm x 25.4 cm, held in an insulated styrofoam container was used as the cooling

Figure 3. Apparatus used to determine temperature preference of slender salamanders.



element. The foam and the redwood leaf litter were saturated with water. The air space inside the box was sprayed with water using an atomizer. The box was then sealed for 1 hour. Relative humidity measurements were taken, prior to and following testing, with a wet-bulb dry-bulb hygrometer. A minimum of 70 percent relative humidity was maintained throughout testing. The heating and cooling elements were placed at opposite ends of the test apparatus and a constant thermal gradient was established, ranging from 0° to 30° C. The gradient was modified until approximately 6 cm wide isotherms were established for the 182.8 cm length. Once established, the resultant scale for the thermal gradient was marked on the inside of the box.

Groups of 50 salamanders were placed in the center of the test apparatus and the cover was replaced. Two hours later the cover was removed and the temperature at each animal's location was recorded with a quick recording mercury thermometer. The location of the isotherms was checked against those previously established. No significant variations in the thermal gradient were observed. Salamanders were returned to the glass jars and maintained for other experiments.

Protean Behavior

The predator escape behavior of slender salamanders was tested using groups of 50 animals (SVL > 33 mm) collected from redwood forest, edge and grassland/disturbed habitats within the study area for the months of April, June and August 1971. These test groups of animals were subjected to 3 types of stimuli: 1) tactile, 2) visual and 3) olfactory. In addition, the various elements of the response were photographically analyzed. The procedure for administering each of the stimuli is described separately.

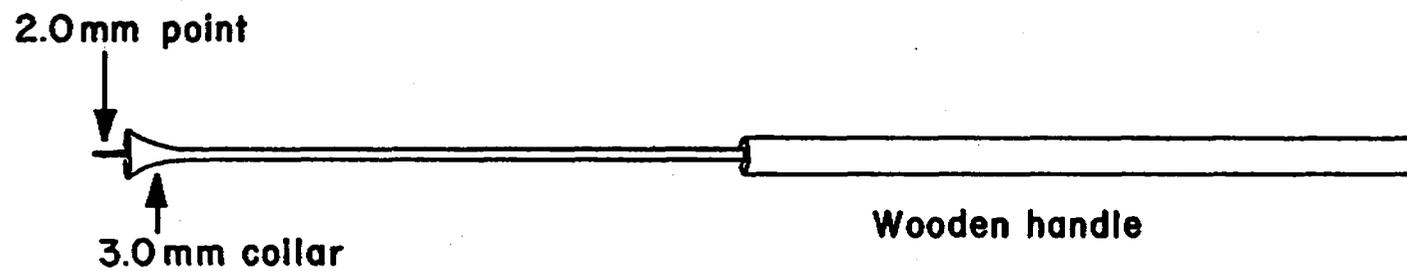
Tactile Response

A wide variety of tactile stimuli were used on slender salamanders to attempt to duplicate the biting action of a potential predator. Following these tests, the stimulus selected consisted of a fine point dissecting pin fitted with a 3-mm collar (Figure 4). The collar consisted of a metal disk glued to the dissecting pin to expose a 2-mm point. The collar allowed the point to be inserted an equal distance into each animal. An effort was made to apply equal pressure each time the stimulus was administered.

Salamanders were tested on a 91.4 cm² plywood board painted dark brown which closely matched their general coloration and that of the soil and leaf litter, since Smyth (1962) and Edmunds (1974) indicated that placing certain amphibians species on a contrasting color surface may significantly modify behavior. To facilitate recording the distance and direction of movement, 1 cm² grid cells were marked on the board. The center of the grid cell board was also marked. Initial tests on the painted surface were unsatisfactory since slender salamanders adhered to the surface and mobility and protean responses were affected. An alternate material was substituted. The grid cell board was covered with a 0.64 cm thick etched glass plate. To reduce adhesion even further the glass plate was lightly sprayed before each test until a uniform fine film of water covered the entire glass surface. The water/etched glass surface allowed the salamanders to move freely and not adhere to the surface. The glass surface also facilitated cleaning prior to each test.

The illumination level was kept at about the same mean light intensity level as measured during overcast conditions in each habitat type: redwood forest, 15 fc; edge, 65 fc; and grassland/disturbed, 330 fc. Salamanders were maintained

Figure 4. Dissecting pin used to administer the tactile stimulus to slender salamanders.



at about 13° C prior to testing. This temperature was chosen based upon evaluation of preliminary temperature tolerance data and was assumed to represent that temperature at which the animals would remain most active (Hendrickson 1954, Anderson 1960, Cunningham 1960).

A uniform intensity tactile stimulus was applied with a downward pressure on the dorsal surface of the salamander. This technique had several advantages: the animal was not able to easily avoid the stimulus and was easily approached without causing the animal to move. However, a distinct disadvantage results from the fact that the downward thrust of the pin momentarily impaled the salamander on the dissecting pin tip and prevented any movement. This problem was increased during the testing of the body and head response. The salamanders frequently did not move when first touched because the downward pressure of the pin allowed no movement. Despite these problems the dorsal surface was chosen as the most acceptable area to administer the tactile stimulus.

The testing procedure consisted of cleaning the glass plate with isopropyl alcohol, thoroughly rinsing it off with tap water and drying. The glass plate was placed on the grid cell board and lightly sprayed with an atomizer containing tap water. Slender salamanders were handled very gently so as not to elicit the protean display. The animals were placed in the center of the grid cell board and covered with a 9.5-cm diameter aluminum film canister for 2 minutes. Covering the salamander provided a quieting effect and minimized the animals attempt to seek cover. The film canister was slowly removed and the tactile stimulus was applied. The distance and direction of the movement were recorded from the center of the grid cell board to the final resting place. The time of the movement was recorded with a manually operated stop watch. Fifty animals from each

habitat were collected and tested in April, June and August 1971. The tactile stimulus was tested on the head, body and tail of salamanders from all habitats in April. Only the tail response was tested in June and August. Each animal was tested once and allowed to recover for 48 hours before additional testing on other body areas was conducted.

Visual Response

The response of slender salamanders to the presentation of potential vertebrate predators was tested using a procedure similar to that described for tactile stimuli. Throughout the course of the study, various potential vertebrate predators were collected from within the study area. The potential predators collected were those associated with the habitat of the slender salamander or were known predators on slender salamanders (Stebbins 1954, 1972). The species and number of predators collected is summarized in Table 3.

The grid cell board, light illumination and glass plate cleaning procedure were as described in the tests of tactile response. The salamander was placed in the center of the grid cell board and covered for 2 minutes with an aluminum film canister. Each of the 63 potential predators were placed in a series of well sealed clear plastic boxes which allowed little or no space for movement. The movements of predators within the box that might be sensed by the salamanders were dampened by adding cotton padding to reduce ground vibrations (Porter 1972:82).

The predator in the sealed clear plastic box was placed to the immediate right of the covered slender salamander. The canister was then slowly removed and the reactions of the slender salamander were noted. A control box which did not contain a predator was also tested. Twenty-five salamanders (SVL > 33 mm) from each habitat type were tested on

Table 3. The species and number of potential vertebrate predators collected within the study area.

Common Name	Scientific Name	Number Collected
<u>Salamanders</u>		
Pacific giant salamander	<u>Dicamptodon ensatus</u>	4
Northwestern salamander	<u>Ambystoma gracile</u>	3
Ensatina	<u>Ensatina eschscholtzi</u>	3
Arboreal salamander	<u>Aneides lugubris</u>	4
Clouded salamander	<u>A. ferreus</u>	3
Black salamander	<u>A. flavipunctatus</u>	3
Rough-skinned newt	<u>Taricha granulosa</u>	3
<u>Lizards</u>		
Western fence lizard	<u>Sceloporus occidentalis</u>	3
Western skink	<u>Eumeces skiltonianus</u>	3
Northern alligator lizard	<u>Gerrhonotus coeruleus</u>	3
<u>Snakes</u>		
Ringneck snake	<u>Diadophis punctatus</u>	3
Racer	<u>Coluber constrictor</u>	2
Gopher snake	<u>Pituophis melanoleucus</u>	1
Common garter snake	<u>Thamnophis sirtalis</u>	3
Western terrestrial garter snake	<u>T. elegans</u>	3
Western aquatic garter snake	<u>T. couchi</u>	3
<u>Moles and Shrews</u>		
Townsend mole	<u>Scapanus townsendi</u>	2
Vagrant shrew	<u>Sorex vagrans</u>	3
<u>Rodents</u>		
Dusky-footed woodrat	<u>Neotoma fuscipes</u>	2
Norway rat	<u>Rattus norvegicus</u>	3
Black rat	<u>R. rattus</u>	1
Deer mouse	<u>Peromyscus maniculatus</u>	5

separate days for each of the 63 potential predators. The salamanders were collected and tested in April 1971.

Olfactory Response

The response of slender salamanders to olfactory stimuli derived from the skin of potential vertebrate predators was tested using a modification of a method developed by Burghardt (1969). The basic method of preparing the chemical extracts began by rinsing off a small quantity of a given predator with tap water. Distilled water in the proportion of 10 cc of water to 1.5 g of the predator was heated to 50° C. The predator was placed in the water and held there for about 2 minutes. The predator was then removed and the resulting extract of its surface substances was centrifuged at 2500 revolutions per minute for 10 minutes. The supernatant liquid was poured into glass vials, fitted with plastic caps and kept refrigerated at about 2.2° C until used. The extracts were very clear and indistinguishable from water, both to the eye and the nose. All extracts for a given test were prepared on the same day of or prior to testing. Once used, any remaining extract was discarded. Extracts were prepared for the 47 amphibian and reptile predators listed in Table 3. Five distilled water controls were also prepared. Mammals could not be tested with this procedure since they would urinate while held in the water. The urine discolored the solution and masked any other body odor that might be present. The resulting extract consisted of urine and feces and was not comparable to the other extracts. Removing all body hair and soaking it may have provided a suitable extract, however, this was not done for this study. Chemical extracts of mammals were not included in this experiment. The extracts were used in the same order indicated in Table 3.

Fifty salamanders from each habitat were collected and tested in May 1971. From each habitat sub-samples of 10 animals each were tested with the chemical extracts derived from each of the 47 predators and the 5 distilled water controls. Each slender salamander was tested once on a given day and allowed a 24-hour recovery period.

The general testing procedure followed the method previously described for tactile stimuli. The vials of chemical extract were removed from the refrigerator and allowed to warm to room temperature, about 20° C. Illumination was maintained at the levels indicated for tactile stimuli. The glass plate was washed with isopropyl alcohol, rinsed with tap water, dried and sprayed with a fine distilled water mist. The slender salamander was placed in the center of the moistened glass plate and covered with the aluminum canister for 2 minutes. The canister was removed and a 0.5 cc drop of the chemical extract was presented to the slender salamander with a 15-cm glass dropper. The drop was placed within 1 to 2 mm of the salamander's head.

The responses were recorded in the following manner. Each animal was allowed 60 seconds to make a response to the extract. If no response was made in that time period, the animal was removed. Slow movement away from the chemical extract was not recorded as a response. If a protean display was elicited, the distance, direction and time of movement were recorded as previously described.

Several attempts were made to determine the receptor organ in slender salamanders responsible for the observed response of the chemical extracts of certain species. Several workers (Brown and Martof 1966, Brown 1968) have suggested that the nasolabial groove of plethodontid salamanders serves directly to facilitate chemoreception. Therefore, an attempt was made to design an experiment which would verify that the olfactory stimulus was transmitted via the nasolabial

grooves to the chemoreceptors of the Jacobson's organs.

Severing the olfactory nerves and physical blockage of the nasolabial grooves were considered. Microsurgery on such a small salamander proved to be too difficult. Attempts to sever the olfactory nerve leading from the nasolabial grooves resulted in severe trauma to the salamanders. Response to all stimuli and handling were significantly reduced following severing of the nerve. Nine of the 10 animals treated died within 2 days following surgery. This approach was abandoned since the surgery significantly affected behavioral response and survival rate.

Physical blockage of the nasolabial grooves was attempted with the following substances: modeling clay, white glue, epoxy glue, silicone caulking compound and petroleum jelly. Each of these substances was gently applied to the nasolabial grooves with a pair of microtweezers. The animals were manually restrained and care was taken not to remove the mucus skin secretions during this procedure. The clay, petroleum jelly and glues did not adhere to the nasolabial grooves and were removed by the natural flushing action of the grooves (Brown and Martof 1966). The silicone caulking compound appeared to remove the mucus skin secretions which resulted in the skin around the nasolabial grooves becoming infected with a fungus-like growth. About 80 percent of the animals treated with the silicone compound died within 3 days. The inability to design an experiment which would impede olfaction but not affect the physiological state of the slender salamander led to the adoption of another experimental design approach.

A test was designed to combine olfactory and tactile stimuli to determine if exposure to the olfactory stimulus would modify the tactile stimulus response. Chemical extracts were used which elicited protean displays. Those animals used included the Pacific giant salamander,

arboreal salamander, ringneck snake, common garter snake, western terrestrial garter snake and western aquatic garter snake. Following the general procedure previously outlined for olfactory and tactile response, slender salamanders were exposed to the extracts of these predators, immediately followed by a tactile stimulus applied to the dorsal surface of the tail.

Fifty slender salamanders were tested with each of the 19 chemical extracts followed by a tactile stimulus. These same animals were tested 2 days later with only a tactile stimulus to the tail. Each animal was tested once a day and allowed to recover for 24 hours between test periods. The direction, distance and time of movement were recorded as previously described.

Photographic Analysis

The protean display exhibited by slender salamanders lasts from 1 to 2 seconds and the components of the display could not be analyzed with the unaided eye. Two mechanical drive Bolex 16-mm movie cameras were used to simultaneously photograph the response of slender salamanders to a low voltage electric shock administered to either the head, body or tail region. Fifty adult salamanders (SVL > 33 mm) were collected in June 1971 from the study area and maintained for several days. Preliminary analysis of the protean displays elicited by tactile stimuli indicated no significant differences between habitats and seasons. These preliminary results led to the combining of habitat types for this experiment.

One camera was mounted vertically and the other horizontally to record both types of movement. The field of vision was about 35 cm for the horizontally mounted camera and 45 cm for the vertically mounted camera. Both cameras

were simultaneously operated by a manual switch. The film used was 16-mm Kodak Tri-X Reversal 7278 with a film speed of 200 ASA. Each camera recorded at 64 frames per second. Indirect illumination was maintained at about 300 fc.

A 25 volt electric shock at 0.4 amperes was delivered through an alternating current variable voltage regulator. Two copper leads, 60 cm in length, were connected to the voltage regulator. Paper clips with sharpened points were attached to the copper leads and used as the contacts. A fixed bracket held the paper clips 0.5 cm apart to avoid spark crossovers and shorting out of the voltage regulator.

The glass plate was placed on a 91.4-cm white mat board with the x and y axis marked in 1 cm increments. A white background was selected to increase photographic contrast. The testing procedure began with cleaning the glass plate with isopropyl alcohol and rinsing it with tap water. The plate was then dried, placed on the white mat board and the plate sprayed with a uniform tap water mist. The salamander was placed at the center of the x-y axis and covered with an aluminum canister for 2 minutes. The canister was gently removed and both cameras were activated immediately prior to the shock being administered. The 2 paper clip probes were quickly slid under that part of the body to be tested. A sample of 50 salamanders was tested on separate days for the head, body and tail response.

Prey Palatability and Toxicity

Force feeding experiments were conducted to determine the toxicity or palatability of slender salamander skin secretions to potential vertebrate predators. Examination of slender salamanders with a dissecting scope revealed that granular venom glands were located along the dorsal ridge from the midbody to the tip of the tail. Very few venom

glands were located on the ventral surface or in the inter-costal region. Based upon the location and concentration of these glands, the dorsal skin of the body and tail were used in force feeding experiments.

A 30-mm section of salamander tail or body was selected as that amount of salamander that would be ingested during a single attack by a predator. Five 30-mm tail and body sections each were fed to all predators on 10 separate days. All test periods were separated by a 4-day recovery period. The methodology used was a modification of a force feeding procedure developed by Brodie (1968b).

All 63 potential predator species listed in Table 3 were tested by feeding either voluntarily or by force, usually the latter. A 30-mm section of slender salamander consisting entirely of either the tail or the body was placed in the animals mouth which was held closed until the animal swallowed. With some of the smaller predators, 3 10-mm sections were force fed separately. With particularly difficult animals, the skin was administered orally in a water solution by means of a blunt needle. The reaction and symptoms of the predators were recorded for a 4-day period following force feeding.

Tail Autotomy

The relationship of the protean display and tail autotomy was tested by recording the reaction of slender salamanders to mechanical severing of the tail. The intent was to determine the behavior of the animal and the response of the severed tail.

Fifty animals (SVL > 33 mm) were each collected from redwood forest and edge habitat and 60 from grassland/disturbed habitat within the study area during April and May 1971. The glass plate and brown grid cell board

previously described were used for this experiment. Indirect illumination was maintained at the following levels for these samples: redwood forest, 15 fc; edge, 65 fc; and grassland/disturbed, 330 fc.

The glass plate was cleaned with isopropyl alcohol, rinsed with tap water, dried and sprayed with a fine water mist before each test. The salamander was placed in the center of the grid cell board and covered with an aluminum canister for 2 minutes. The canister was slowly removed and the tail was immediately severed using an X-ACTO knife fitted with a No. 3 blade. The tail was severed about 1 cm posterior to the hind limbs. Blades were changed frequently to eliminate ragged cuts or unnecessary tearing of the skin. The time, distance and direction of the movement of the salamanders and the severed tails were recorded.

Predator-Prey Interactions

All 63 predators listed in Table 3 were used to test the response of slender salamanders (SVL > 33 mm) to an actual attack by a predator. A small observation enclosure was constructed to contain both predator and prey. The enclosure used the 91.4 cm² grid cell board and glass plate as the bottom and was contained with plywood sides 61 cm in height. The inside surface of the enclosure was dark brown. This color was selected to match as closely as possible the natural ground cover on which slender salamanders are normally collected. In addition, the matching color did not give the predator an unfair advantage by highlighting a dark prey upon a light background. Illumination level was maintained at about 65 fc for all test animals.

Prior to testing, amphibian and reptile predators were not fed for 14 days. Shrews and moles were not fed for 6 hours and rodents for 24 hours. These time periods insured

that the predators were hungry but not noticeably weakened. The glass plate was cleaned with isopropyl alcohol, rinsed with tap water, dried and sprayed with a water mist before each test. The general testing procedure followed those previously described. The slender salamander was gently placed in the center of the enclosure and covered with an aluminum canister for 2 minutes. During this period the predator was placed in the corner of the enclosure and allowed to move about freely. The canister covering the slender salamander was slowly removed and both predator and prey were allowed to interact. Predator and prey were observed for 30 minutes and any significant behavioral responses were recorded. One slender salamander was presented to each predator on a given day. A total of 10 slender salamanders were individually presented to each of the 63 predators.

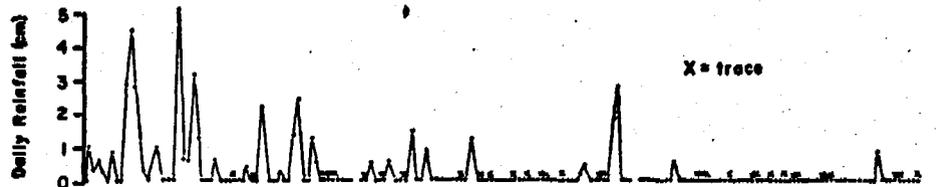
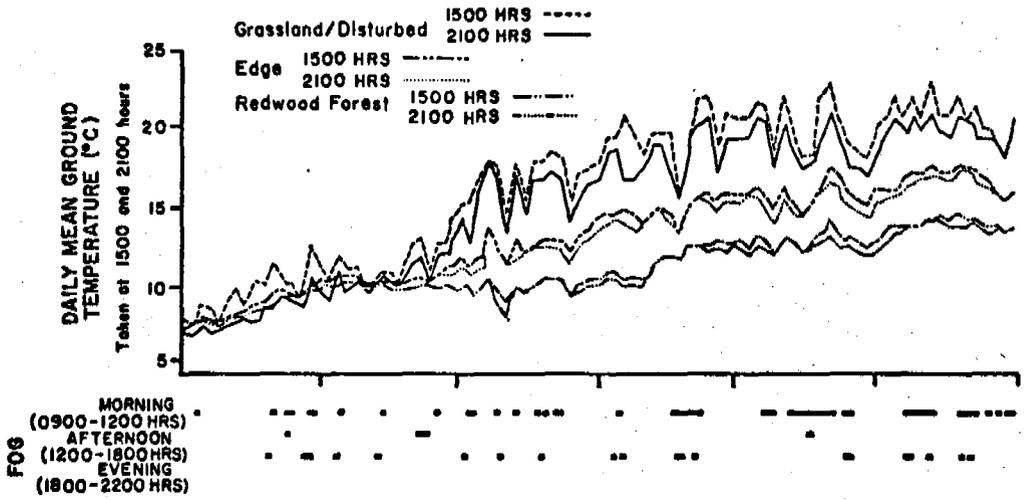
IV. RESULTS

Surface Activity Patterns

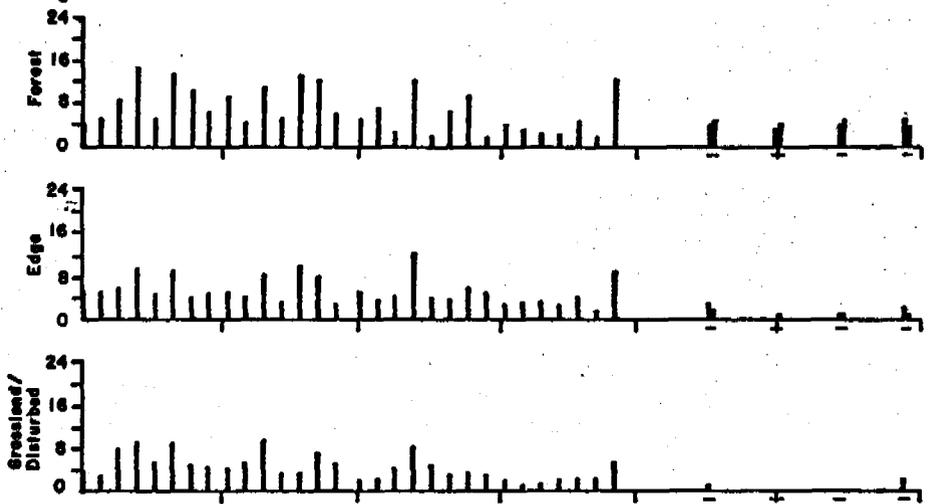
Differences were noted in surface activity of slender salamanders between months, habitat types, and diurnal and nocturnal samples. Figure 5 summarizes the relationship of rainfall, ground temperatures and fog with diurnal and nocturnal surface activity in all habitats from March through August 1971. Surface activity was positively correlated with rainfall and ground temperatures ranging from 7.2° to 16.9° C. Similar correlations have been reported by Hendrickson (1954), Anderson (1960) and Maiorana (1971, 1974). Hendrickson (1954:12) reported surface activity within a temperature range of 4.4° to 15.5° C. Since this study did not include the coldest months of the winter, January and February (U.S. Weather Bureau 1960), the full range of ground temperatures was not recorded. The effects of low ground temperatures on surface activity could not be evaluated since no freezing or near freezing temperatures were recorded. Hendrickson (1954:11) noted that near or below freezing ground temperatures were avoided by the animals going underground.

In general, elevated ground temperatures operated in concert with periods of low rainfall to decrease surface moisture and create an unsuitable foraging environment for slender salamanders (Maiorana 1971). As ground temperatures in the grassland/disturbed habitat approached about 20° C diurnal surface activity ceased. This increase in ground temperature was also closely associated with a decrease in daily precipitation. The higher ground temperature observed in the grassland/disturbed and edge habitats was due to the reduced tree and shrub canopy. In redwood forest habitat

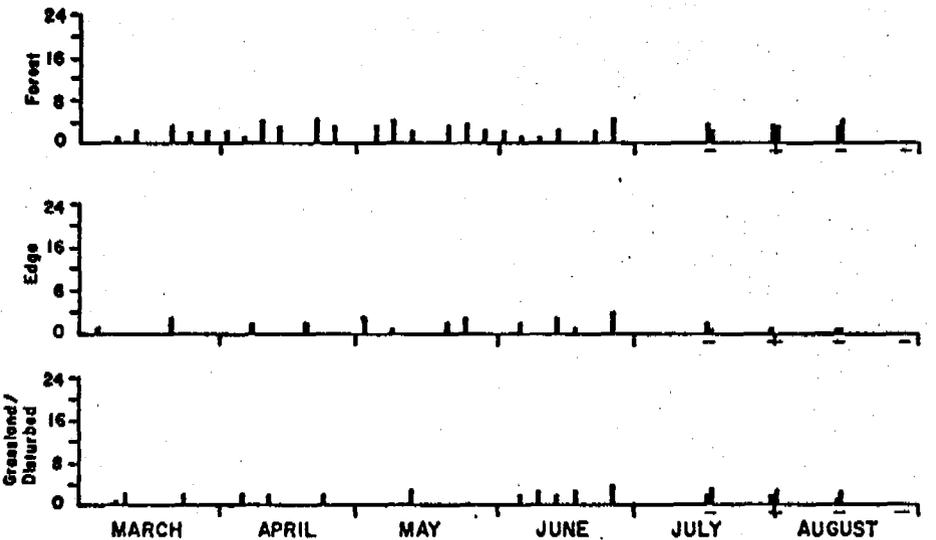
Figure 5. The diurnal and nocturnal abundance of slender salamanders in the redwood forest, the edge and the grassland/disturbed habitats with respect to rainfall, ground temperatures and fog, March through August 1971.



NUMBER OF ANIMALS IN DIURNAL SAMPLE (1500-1700 HRS)



NUMBER OF ANIMALS IN NOCTURNAL SAMPLE (2000-2200 HRS)



MARCH APRIL MAY JUNE JULY AUGUST

this tree and shrub canopy maintains lower ground temperatures and higher relative humidity.

Ground temperatures were relatively uniform in the redwood forest habitat and from March through August ranged from 7.0° to 14.5° C. During this same period, little variation was observed between diurnal and nocturnal ground temperatures. In edge habitat differences in diurnal and nocturnal temperatures were minimal from March through May but varied from 0.0° to 0.5° C from June through August. The overall temperature range observed in edge habitat was 7.0° to 17.0° C. The grassland/disturbed habitat displayed the greatest temperature range, 7.0° to 23.0° C. From March through August differences in diurnal and nocturnal temperatures ranged from 0.0° to 2.0° C.

The relationship between rainfall and ground temperature was best demonstrated in redwood forest habitat during April and May. Ground temperatures averaged about 10.0° C for both months but rainfall patterns were irregular. During periods of heavy rainfall, surface activity increased about 50 percent over periods with little or no rainfall. This relationship also existed in edge and grassland/disturbed habitat, but was not as pronounced. The rainstorm recorded on June 25-26 also indicates the relationship of ground temperature and rainfall. No significant rainfall was measured for 30 days prior to this storm. Surface activity had begun to decline in all habitat types. During the rainstorm, diurnal and nocturnal surface activity increased from 100 to 400 percent over the previous sample. Ground temperatures only decreased from 0.5° to 2.0° C during this same period. In the grassland/disturbed habitat the effects of elevated ground temperatures appear more significant during late spring and summer. Ground temperatures greater than 20° C exceed the critical thermal limits for this species (Brattstrom 1963). Diurnal surface activity was virtually

eliminated above this temperature (Figure 5). The more rapid increase in ground temperatures of grassland/disturbed habitat following periods of low rainfall indicates the moderating effects of tree and shrub canopy cover on ground temperatures and consequently on soil and leaf litter moisture as well.

The relationship of fog and surface activity is obscured by the frequent simultaneous occurrence of fog and precipitation from March through May. However, from June through August fog usually occurs without measurable precipitation. Fog occurred at least once a day during 50 percent of July and August. However, no peaks in surface activity could be related to the occurrence of fog during this time period. Additional samples during the summer months would have been required to detect a correlation between fog and surface activity.

Tree canopy has been indicated as an important factor modifying both ground temperatures and relative humidity (Waring and Major 1964). Figure 6 shows the mean light intensity measurements for all sampling areas. Table 4 compares light intensity measurements between full sun and overcast conditions within and between habitats. In redwood forest, the standard deviation for overcast and full sun measurements was small, 3.3 and 5.1 respectively. Standard deviation increased in edge and grassland/disturbed habitats owing to the increased variability of canopy cover conditions and exposure to full sun.

Mean light intensity for overcast and full sun conditions was highest in grassland/disturbed habitat (331.4 to 806.8 fc) and decreased in edge habitat (65.5 to 87.5 fc) and redwood forest (15.4 to 21.6 fc). Comparison of Figures 5 and 6 indicate the relationship between increased tree or shrub canopy cover, decreased ground temperatures and the resultant

Figure 6. A comparison of the mean light intensity under full sun and overcast conditions for each of the 11 sampling areas in the redwood forest, the edge and the grassland/disturbed habitats.

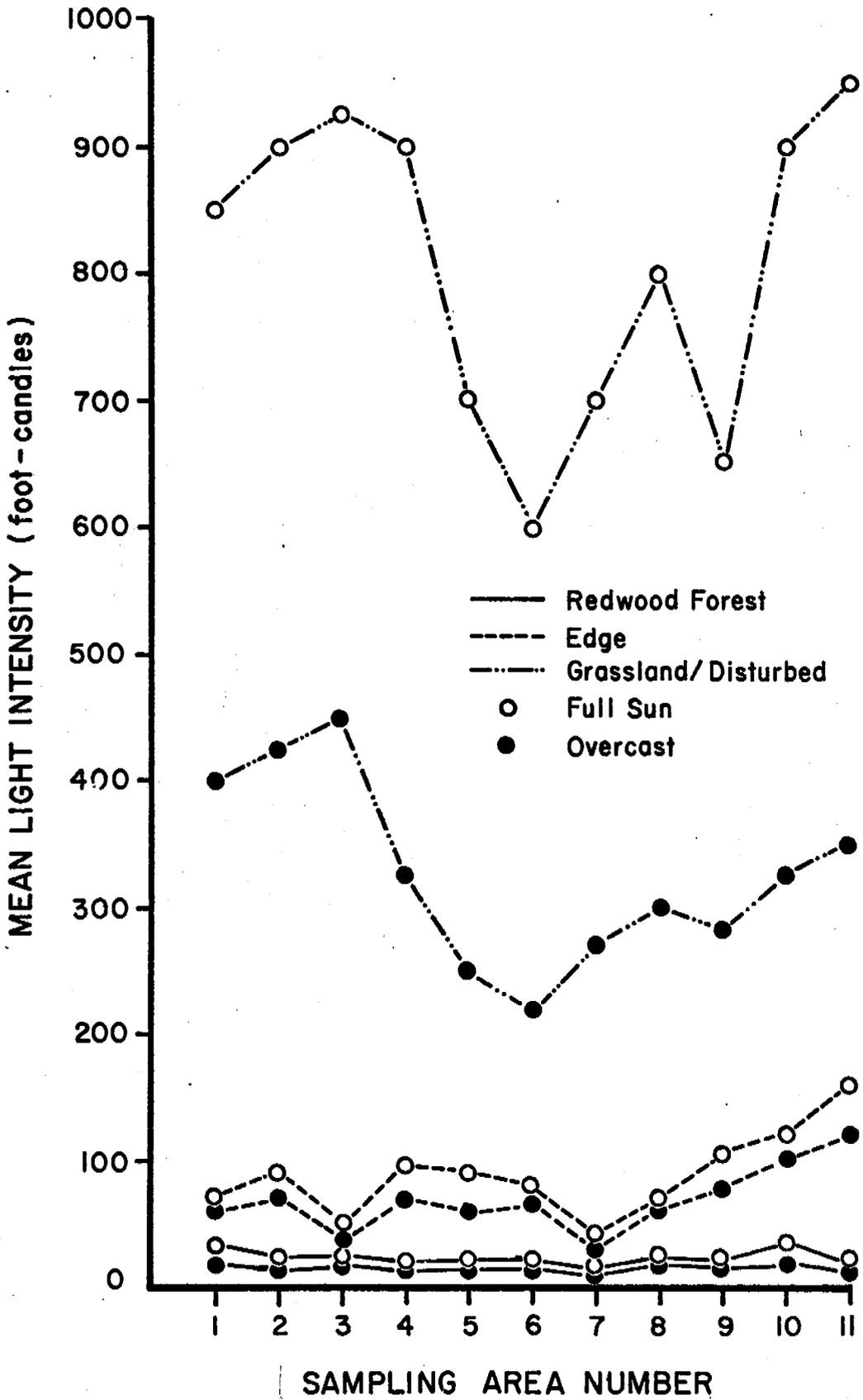


Table 4. A comparison of the mean and standard deviation of light intensity measurements and the percent increase in the mean between full sun and overcast conditions within and between habitats. The mean represents all 11 sampling areas in each habitat. Symbols: \bar{x} , mean; SD, standard deviation.

Habitat Type	Light Intensity (fc)		Percent Increase in Mean Light Intensity <u>1/</u>	
	\bar{x}	S.D.	Within Habitat	Between Habitats
Redwood Forest				
Overcast	15.4	3.3	-- <u>2/</u>	--
Full sun	21.6	5.1	40.3	--
Edge				
Overcast	65.5	27.3	--	325.3
Full sun	87.5	33.7	33.6	305.1
Grassland/Disturbed				
Overcast	331.4	75.0	--	405.9
Full sun	806.8	123.5	143.5	822.1

1/ Comparisons are between successively more open habitat types; redwood forest and edge and edge and grassland/disturbed.

2/ Represents the lowest light intensity condition.

increase in soil moisture which allows slender salamanders to remain active on the surface.

Figure 7 is a comparison of the monthly mean number of animals active during the diurnal and nocturnal samples from March through August 1971. Diurnal surface activity declined in all habitats from March through June and began to stabilize at a lower level in July and August. Analysis of mark-recapture data indicated that the same animals were active throughout the entire study period but at a reduced level from June through August. Twenty-one percent of the animals captured during March through May were recaptured once during the period June through August.

Nocturnal activity remained relatively constant throughout the study period. From June through August nocturnal activity approached or equaled diurnal activity in the redwood forest type and edge habitats and was greater in the grassland/disturbed habitat. About 18 percent of the animals active during the nocturnal samples during the March through August period were also found at least once during the diurnal samples of the same period. Diurnal and nocturnal surface activity of juvenile animals was not observed after mid-May in all habitats. No other age class difference between diurnal or nocturnal activity or habitats was noted.

Figures 8, 9 and 10 show the monthly mean number of salamanders found during the diurnal and nocturnal samples in each habitat type. Standard deviation is shown to indicate variability of the monthly data. A comparison of Figures 8, 9 and 10 shows significantly less ($P < 0.05$) seasonal variation and a consistently smaller standard deviation in nocturnal than in diurnal surface activity. Reexamining individual sampling areas several times during both the diurnal and nocturnal samples indicated no significant difference in the ability to detect slender salamanders during either period.

Figure 7. A comparison of the diurnal and nocturnal monthly mean number of slender salamanders occurring in the redwood forest, the edge and the grassland/disturbed habitats, March through August 1971. Monthly mean number of animals indicates the mean number recorded per sample for each month.

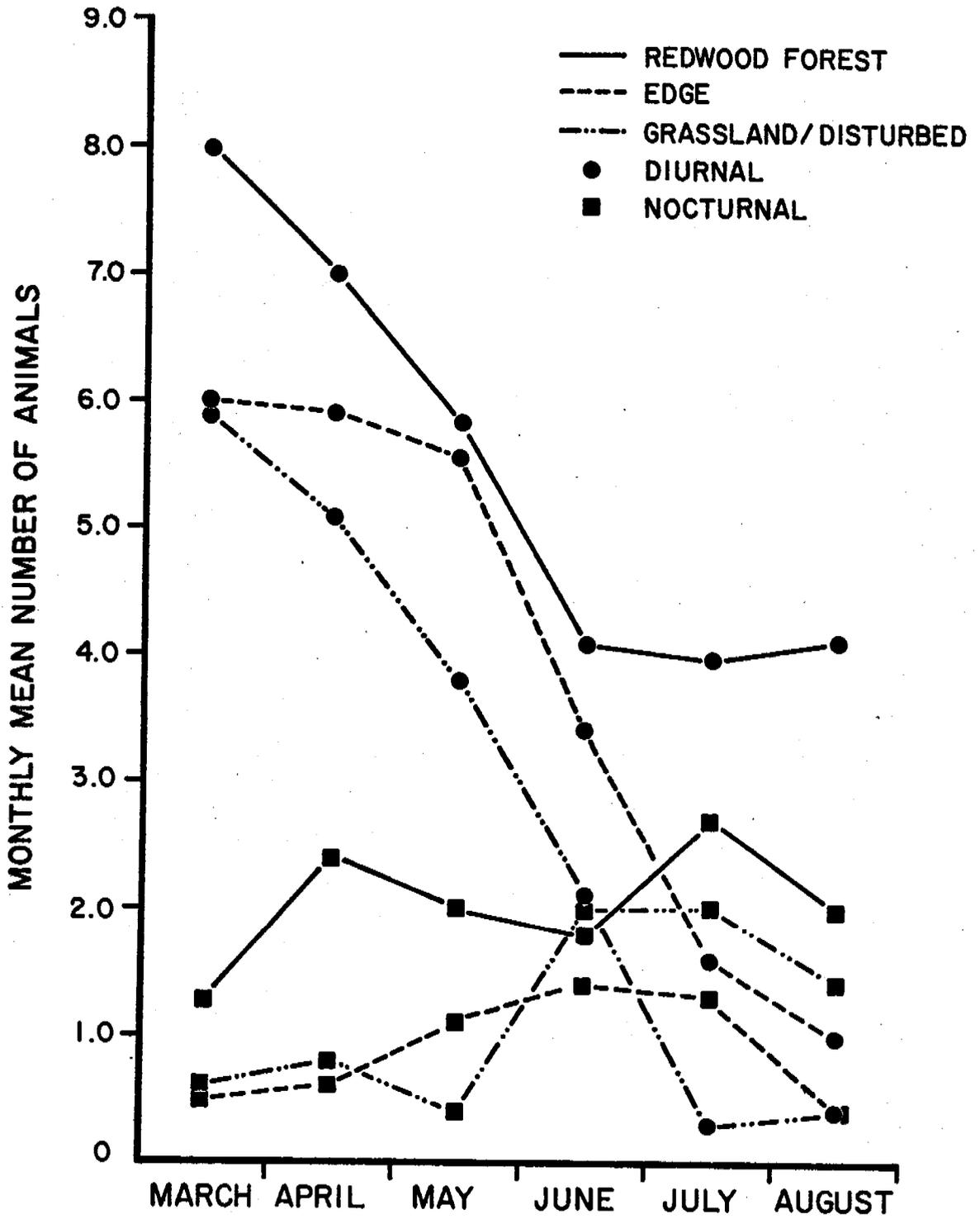


Figure 8. A comparison of the diurnal and nocturnal monthly mean number of slender salamanders occurring in the redwood forest, March through August 1971. Monthly mean number of animals indicates the mean number recorded per sample for each month. Symbols: horizontal line, mean; rectangle, standard deviation \pm mean.

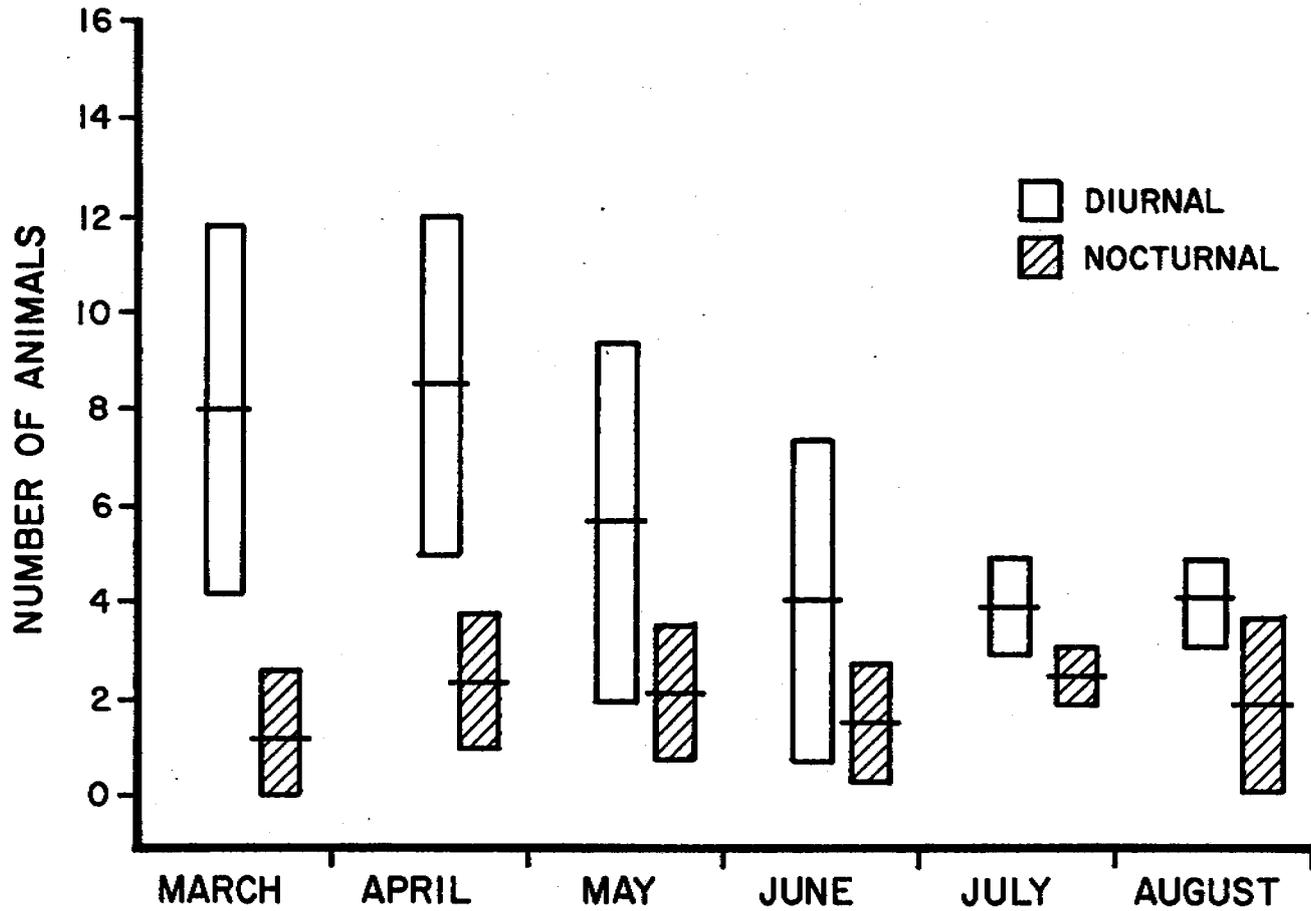


Figure 9. A comparison of the diurnal and nocturnal monthly mean number of slender salamanders occurring in the edge habitat, March through August 1971. Monthly mean number of animals indicates the number recorded per sample for each month. Symbols: horizontal line, mean; rectangle, standard deviation \pm mean.

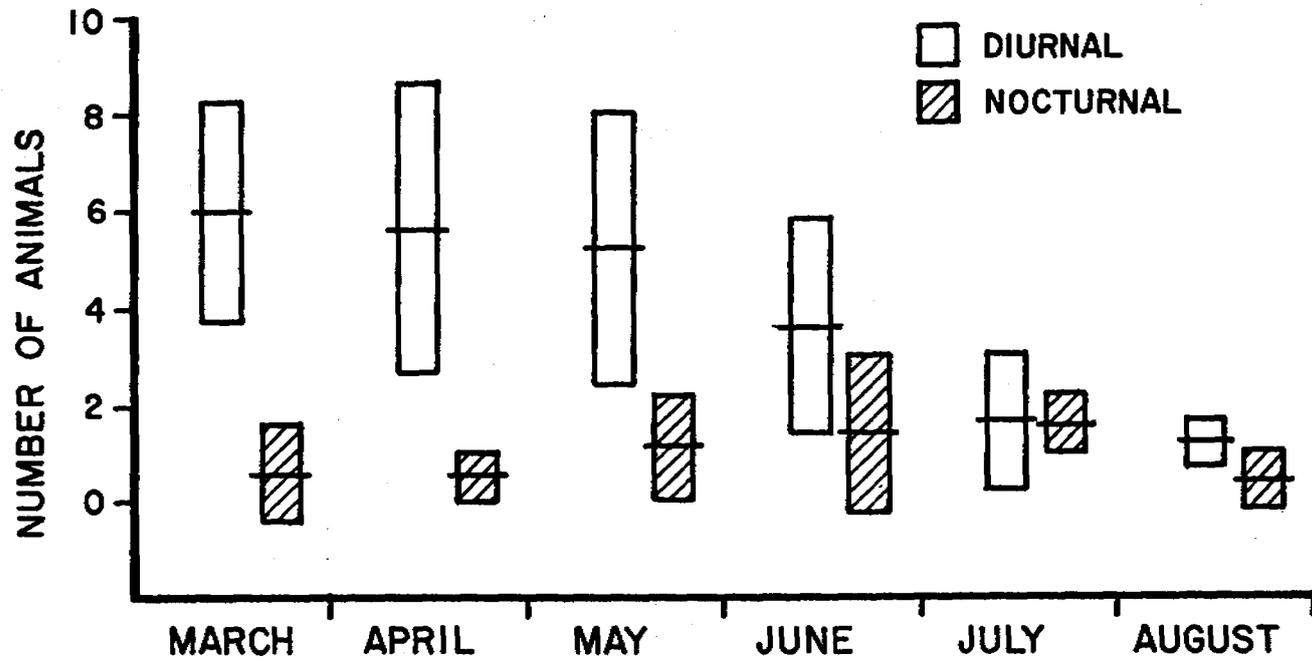
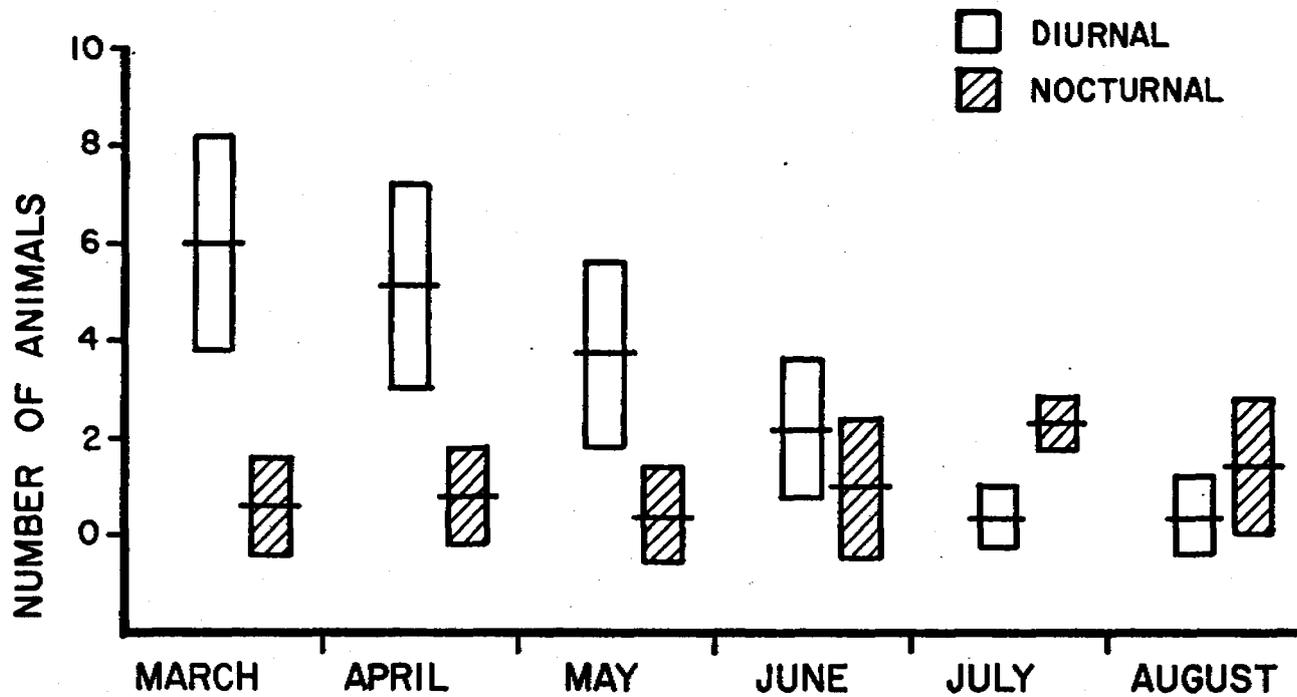


Figure 10. A comparison of the diurnal and nocturnal monthly mean number of slender salamanders occurring in grassland/disturbed habitat, March through August 1971. Monthly mean number of animals indicates the number recorded per sample for each month. Symbols: horizontal line, mean; rectangle, standard deviation \pm mean.



Analysis of mark-recapture data indicated that monthly mean distance moved from the original capture point varied with habitat and season. A total of 668 slender salamanders was collected and marked during this study. Of the 668 animals 487 (72.9%) were not recaptured and 93 (13.9%) were recaptured once (Table 5). The distances moved from the original capture points for all recaptured animals were averaged for each month. Throughout the study period, monthly mean distance moved was roughly equivalent in redwood forest and edge habitats, but was 38 percent lower in grassland/disturbed habitat (Figure 11). The monthly mean distance moved decreased at approximately the same rate in all 3 habitats. No age class difference in the monthly mean distance moved could be detected between habitats or seasons.

Hendrickson (1954) and Anderson (1960) reported home range movements averaging 152 cm for 82 percent of the total moves recorded. They did not report on any seasonal variations. Hendrickson's (1954) estimates of home range were based on cumulative analysis of 3 years' data and Anderson's (1960) was derived from a 14 to 32 day period. Anderson (1960) reported increased mobility of juveniles but no sex differences related to home range. Hendrickson (1954) indicated neither a sex nor age class difference associated with home range movements.

The monthly percentage of protean displays exhibited by slender salamanders during the diurnal and nocturnal samples is shown in Figure 12. Only protean displays consisting of violent random lateral movements were recorded. The serpentine movement frequently used by slender salamanders to escape into the leaf litter was not included in the data shown in Figure 12. Protean displays decreased in all habitats from March through August. No relationship between habitat types appears to exist. Separate analysis of nocturnal and diurnal samples indicated no significant

Table 5. Recapture frequencies for slender salamanders marked in the redwood forest, the edge and the grassland/disturbed habitats from March through August 1971.

No. Animals Marked	No. Times Recaptured
487	0
93	1
74	2
4	3
7	4
2	5
0	6
1	7
Sub total <u>181</u>	
Total 668	

Figure 11. Monthly mean distance moved by slender salamanders in the redwood forest, the edge and the grassland/disturbed habitats, March through August 1971.

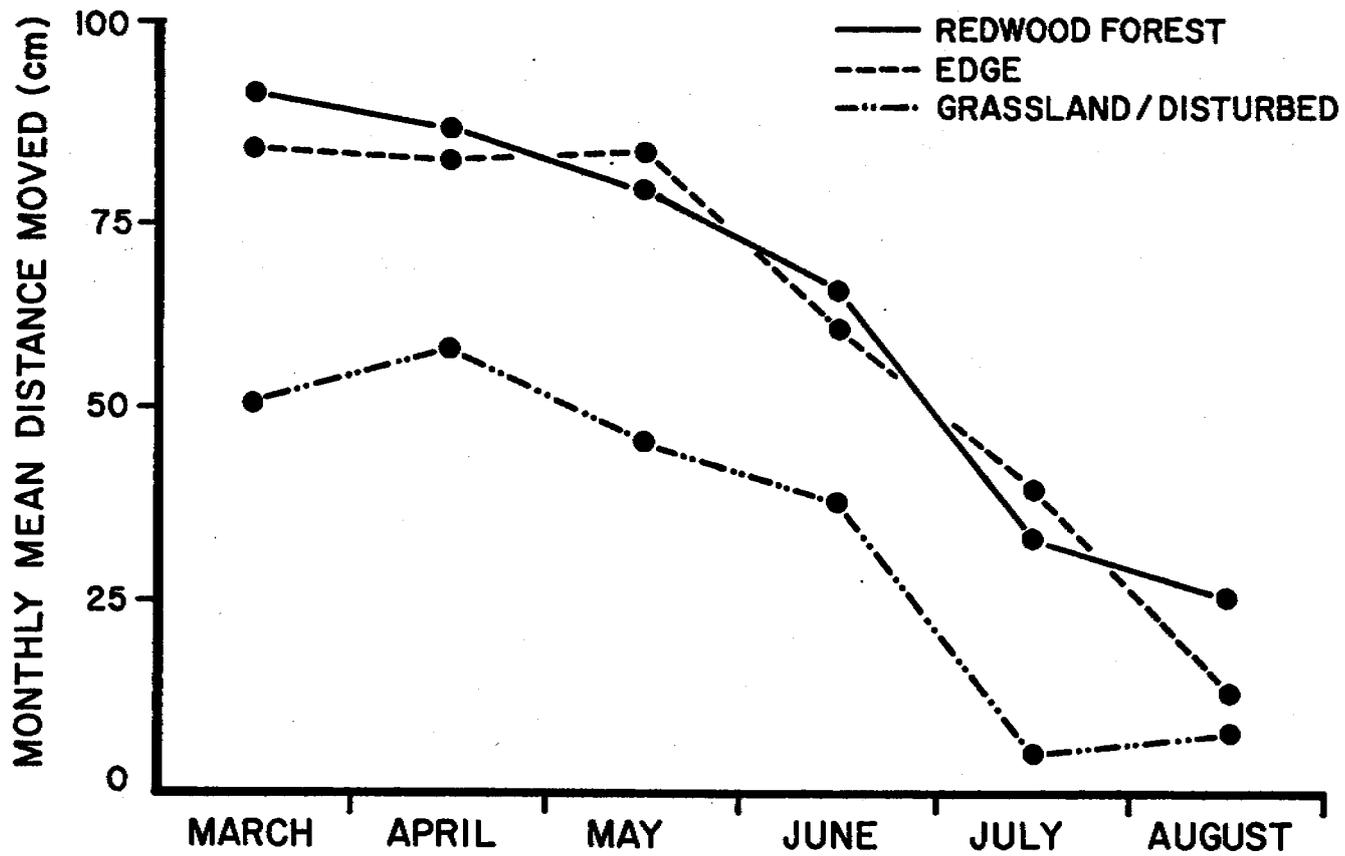
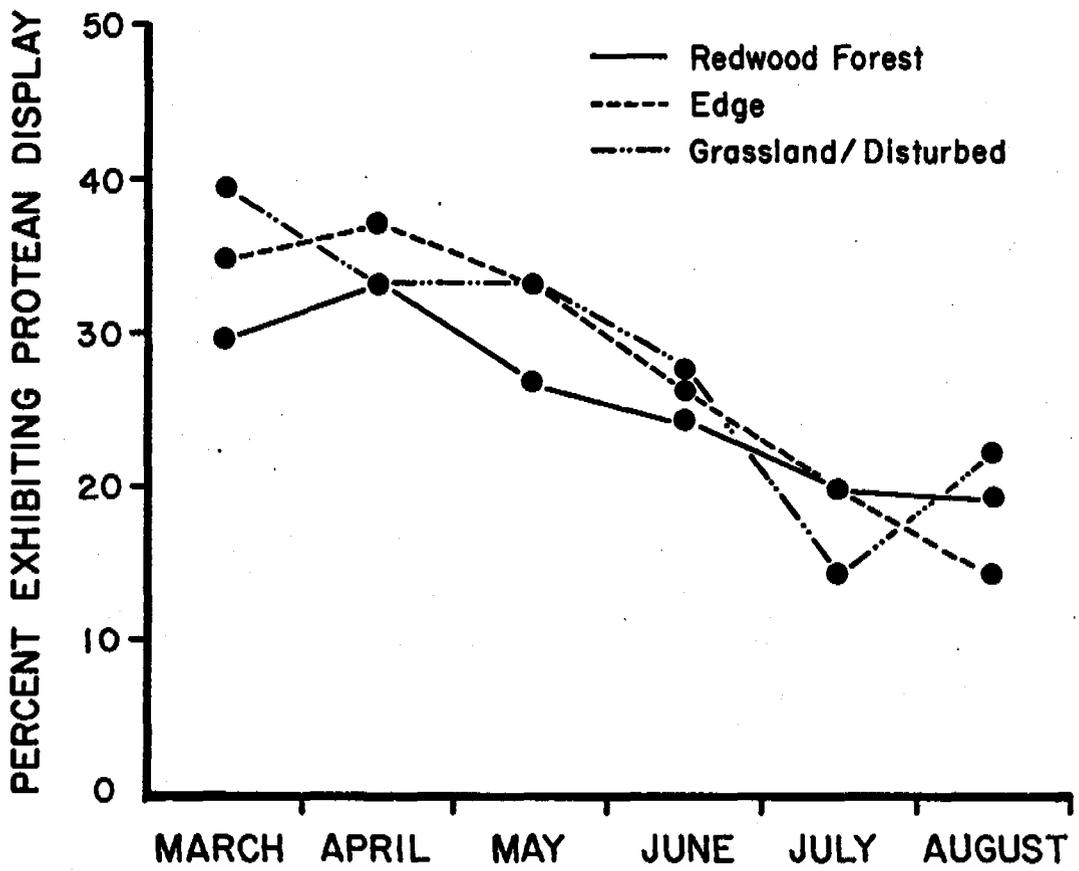


Figure 12. Monthly percentage of slender salamanders exhibiting protean displays while being collected in the redwood forest, the edge and the grassland/disturbed habitats, March through August 1971. Diurnal and nocturnal samples are combined.



differences in the monthly percentages of animals exhibiting protean displays. Comparisons of age class, habitat and number of protean displays showed no apparent relationships.

Analyses of recapture data and protean displays indicated that the following percentages of protean displays were recorded with these recapture frequencies: 0 recapture, 67 percent; 1 recapture, 36 percent; 2 recaptures, 25 percent; 3 recaptures, 0 percent; 4 recaptures, 0 percent. The number of 0, 1 and 2 recaptures were evenly distributed from March through August.

Figure 13 indicates the percentage of animals handled for the first time which exhibited protean displays, March through August 1971. The lack of significant change in the percentage of protean displays from May through June suggests that the change in handling technique at this time did not affect the number of protean displays reported. The decrease in the number of protean responses was observed in first time captures and first and second time recaptures.

The monthly percentage of animals with regenerating or absent tails for the combined diurnal and nocturnal samples is presented in Figure 14. Separate analysis of diurnal and nocturnal samples indicated similar relationships between months and habitats. From March through August the number of animals with regenerating or absent tails increased 153 percent in redwood forest and 500 percent in edge and grassland/disturbed habitats. The percent of regenerating or absent tails in grassland/disturbed and edge habitats increased sharply in July and August; however, in redwood forest only increased moderately. From March through August the percentage of animals with regenerating or absent tails in all habitats ranged from 24.3 to 73.9. Similar percentages were reported by Hendrickson (1954), Anderson (1960) and Maiorana (1974).

Figure 13. Monthly percentage of slender salamanders exhibiting protean displays during the first capture, March through August 1971. All habitats are combined.

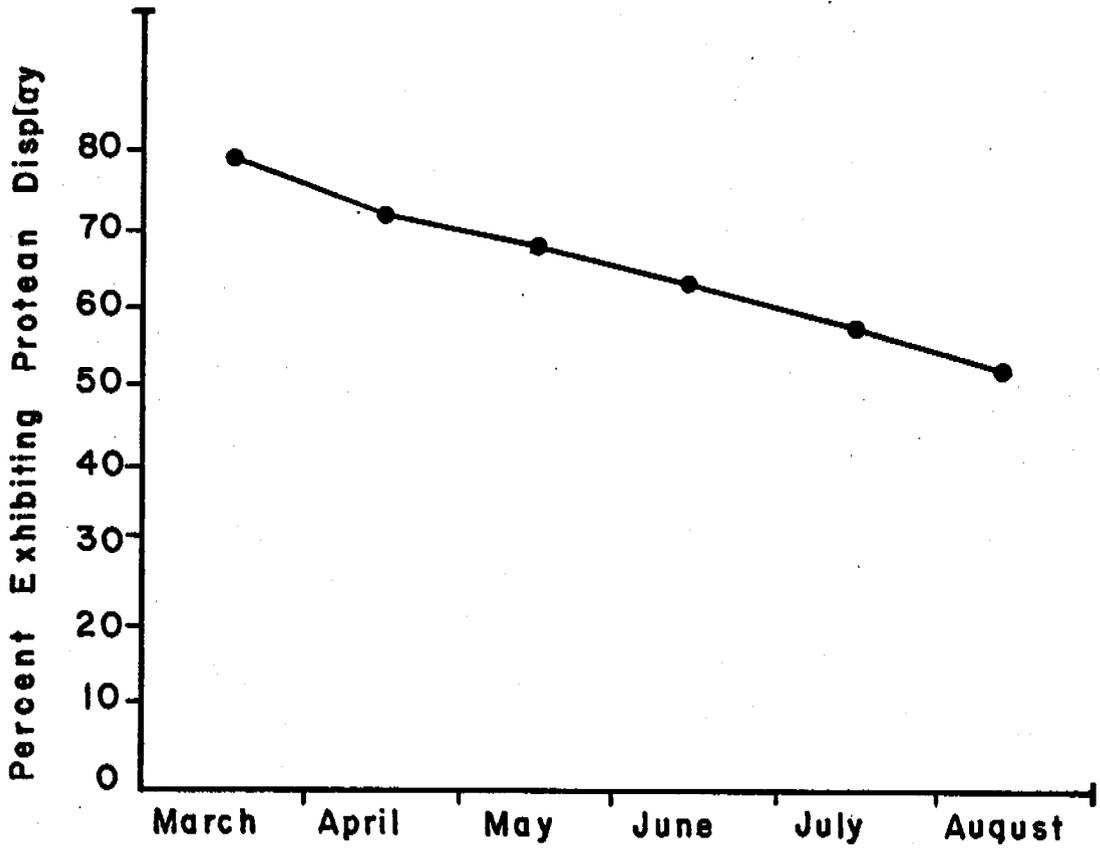
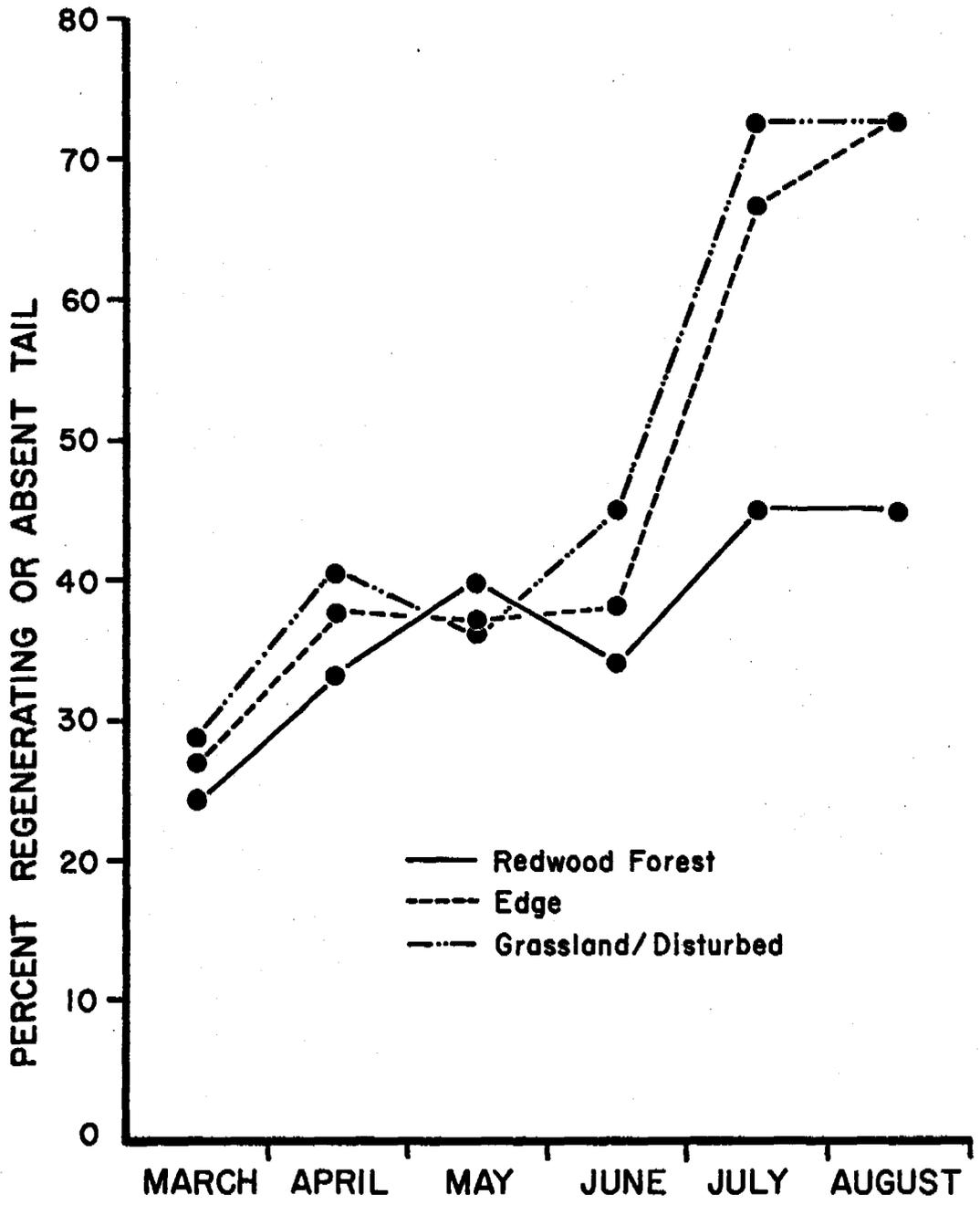


Figure 14. Monthly percentage of slender salamanders with absent or regenerating tails in the redwood forest, the edge and the grassland/disturbed habitats, March through August 1971.



The relationship of the watch-spring-coil posture of slender salamanders at rest and the ground temperatures at which they were collected is indicated in Figure 15. Ninety-three percent of the animals were found between 7° to 10° C. All of these animals were found under cover objects. This posture was not observed in animals collected in the leaf litter. No animals in the coiled posture were collected from June through August. Figure 16 shows the monthly number and percentage of coiled animals in all habitats during the diurnal and nocturnal sampling conducted from March through May.

During March the monthly mean percentage of coiled animals was 35.8 ± 2.5 for the diurnal sample and 65.9 ± 1.4 for the nocturnal sample. In April the monthly mean percentage of animals found in the coiled posture in all habitats was 28.9 ± 11.7 for the diurnal sample and 71.1 ± 11.7 for the nocturnal sample. In May all of the coiled animals were found during the nocturnal sample. The percent decrease in coiled animals from March through May for each habitat was as follows: redwood forest, 83.3 percent; edge, 92.8 percent; and grassland/disturbed, 91.7 percent. The reduction in numbers of coiled animals from March through May and the decrease in the diurnal sample correlated with lower ground temperatures (7° to 10° C) recorded at these times in each habitat.

Temperature Preference

Temperature preference in slender salamanders under conditions of relative humidity greater than 70 percent is summarized for the 3 habitat types for April, June and August 1971 (Figure 17). Mean temperature preference ranged from 12.7° to 12.8° C. No significant difference ($P < 0.05$) existed between habitat types. At 70 percent humidity

Figure 15. Number of slender salamanders displaying coiled posture at various ground temperatures during March and April 1971.

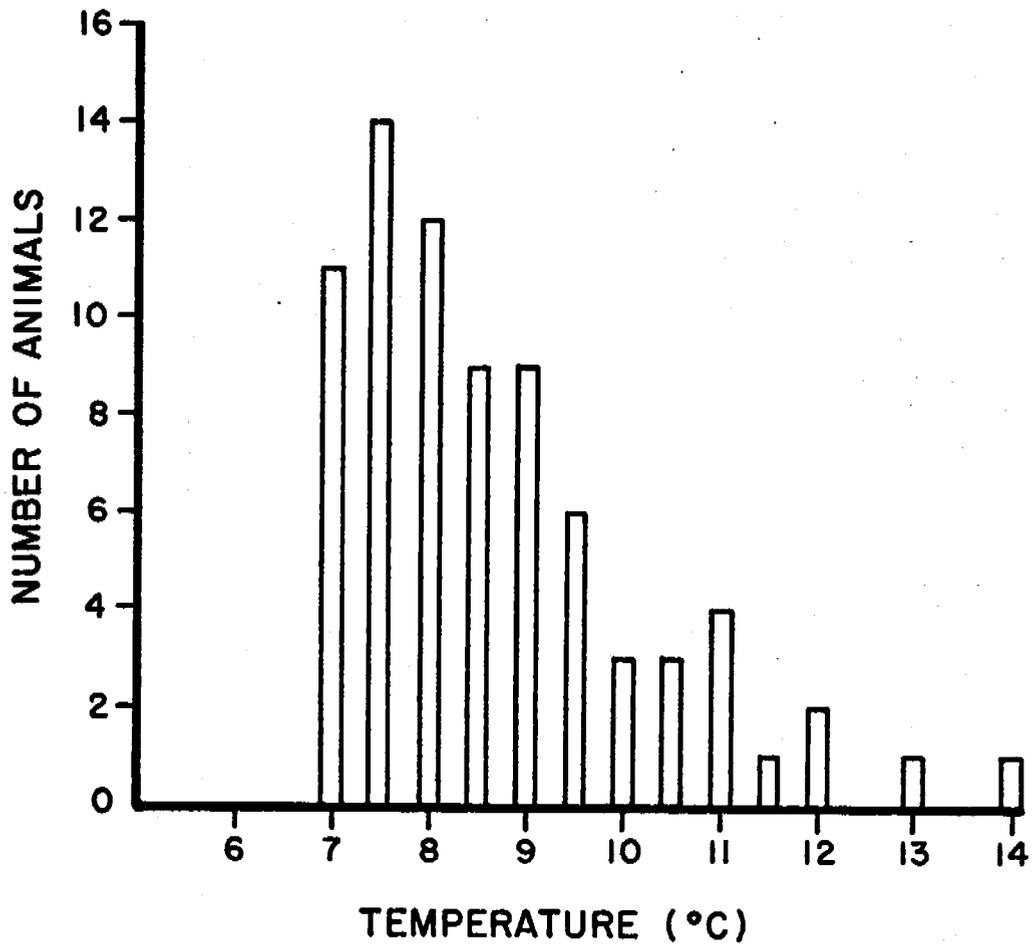


Figure 16. Monthly number of slender salamanders displaying coiled posture in the redwood forest, the edge and the grassland/disturbed habitats, March through May 1971. The monthly percentage of the total number of coiled animals found during the diurnal and nocturnal samples is shown within each histogram.

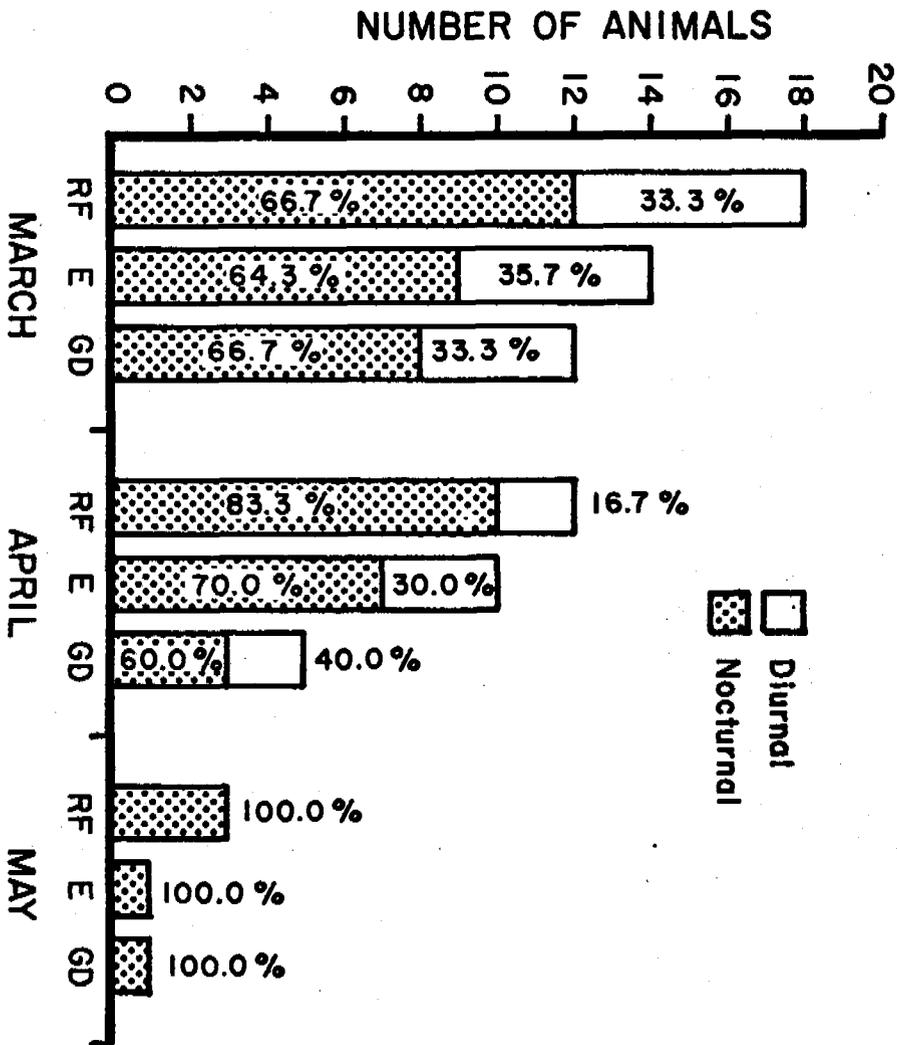
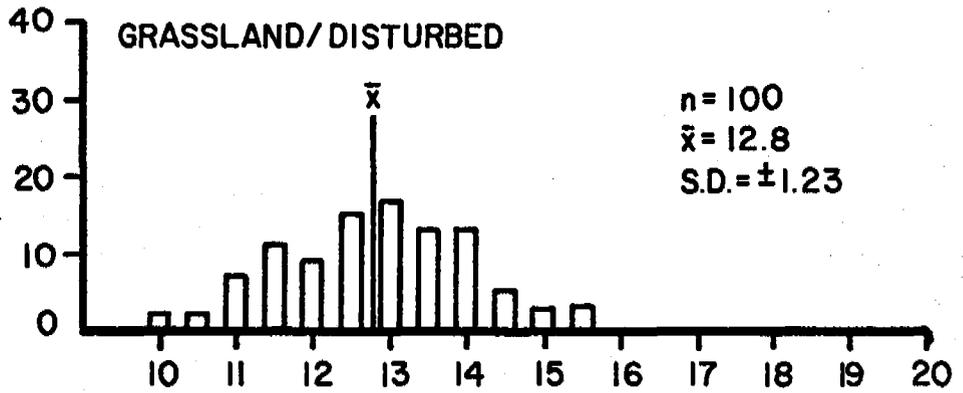
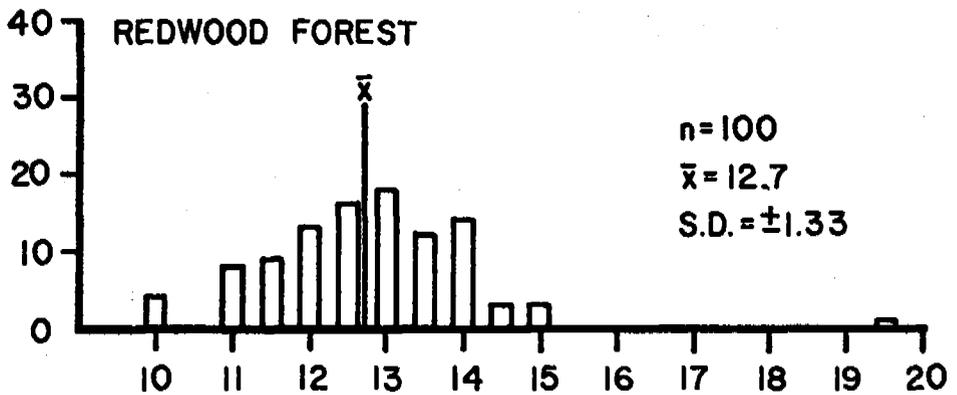
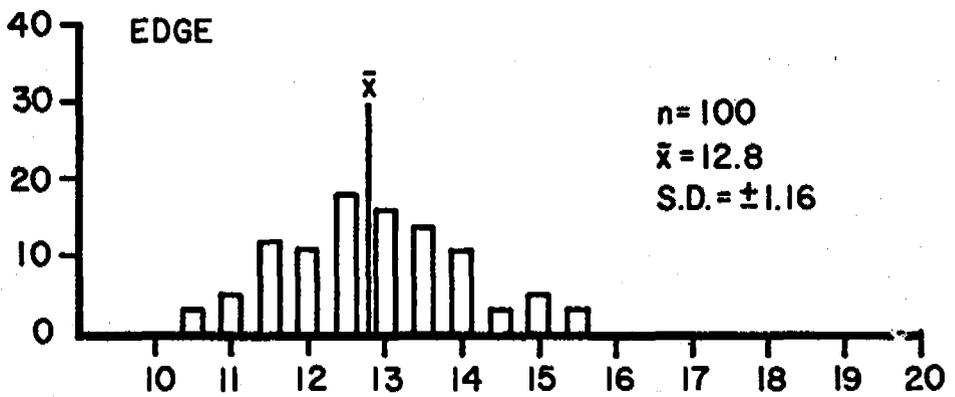


Figure 17. Frequency distribution of slender salamanders with respect to temperature at a relative humidity greater than 70 percent. Animals were collected in redwood forest and tested in April 1971. Symbols: n , sample size; \bar{x} , mean; SD, standard deviation \pm mean.



NUMBER OF ANIMALS



TEMPERATURE (°C)

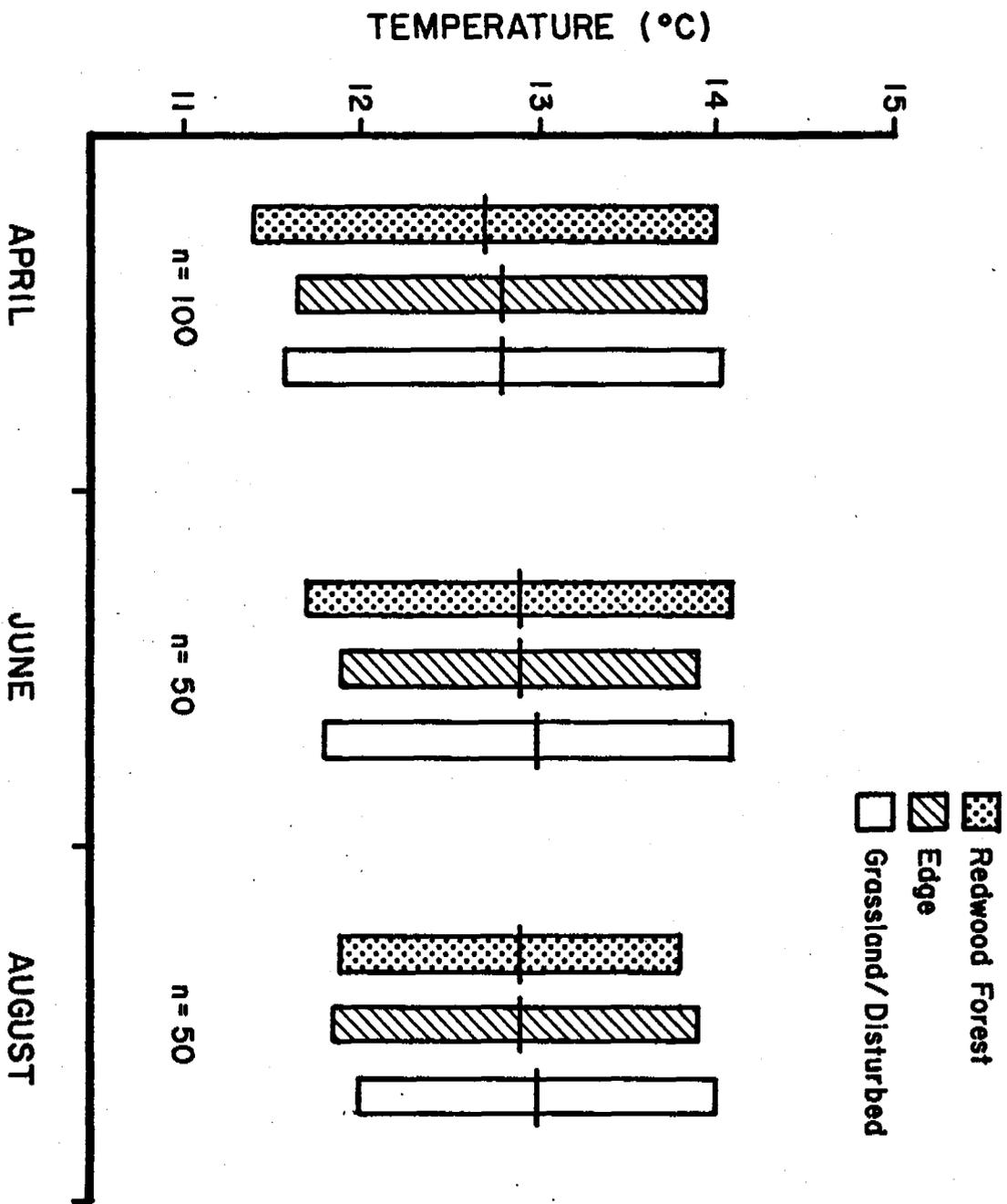
this species appears to thermoregulate between 10.0° and 15.5° C.

One individual from the April redwood forest sample adhered to the metal bottom of the test apparatus at the 19.5° C point and died during the experiment. Average ground temperatures for April in the redwood forest were about 10.0° C. The exposure of this animal to a 95 percent increase in temperature may have resulted in heat stress. Maiorana (1977) reported significant mortality in slender salamanders following exposure to temperatures exceeding 20° C.

Brattstrom (1963) reviewed the thermal tolerance of Batrachoseps on the basis of ground temperatures taken throughout its range. The temperatures ranged from 7° to 21° C with a mean of 12.5° C. Individual species' temperatures ranges and means were not presented. Approximately 86 percent of the slender salamanders collected from March through August were collected at ground temperatures within the 10 to 15.5° C range. Those animals active outside this range were found under cover in moist conditions. Although relative humidity decreases during the summer months (U.S. Weather Bureau 1960), relative humidity within the leaf litter, upper soil layer and under cover objects usually remains quite high (Waring and Major 1964, Maiorana 1974, 1977).

Figure 18 shows the mean and standard deviation for animals tested in April, June and August 1971, for all habitat types. No significant differences ($P < 0.05$) existed between habitats or months.

Figure 18. A comparison of the mean temperature preference of slender salamanders tested in a thermal gradient at a relative humidity greater than 70 percent. Animals were collected in the redwood forest, the edge and the grassland/disturbed habitats during April, June and August 1971 and tested during these same months. Symbols: n, sample size; horizontal line, mean; rectangle, standard deviation \pm mean.



Protean Behavior

Tactile Response

Protean displays in slender salamanders were elicited by tactile stimuli administered to the tail, body and head. Figure 19 shows the direction, distance and time of movement for slender salamanders receiving a tactile stimulus (pin prick) on the dorsal surface of the tail. These animals were collected in redwood forest habitat and tested in April 1971. All 50 animals tested responded with protean displays. The direction of movement from the stimulus contact point was random. No significant differences were noted between the expected and observed number of responses directed to quarters 1 - 4 of Figure 19 ($\chi^2 = 0.72$, 3 df, $P < 0.05$).

Figure 20 shows the relationship between time and distance of movement for the data shown in Figure 19. Linear regression analysis of the relationship between time and distance of movement indicated a significant correlation ($r^2 = 0.347$, $P < 0.05$). Within a single protean display, movement was frequently directed away from and toward the tactile stimulus. Random movement from a starting point for a finite period of time increases the probability that the salamander will increase the distance from that starting point. Comparison of the mean time of movement, 1.02 ± 0.28 s and mean distance moved 11.5 ± 5.13 cm indicates a consistent response time with greater variance in the distance moved. These same relationships were noted in responding animals for tactile stimuli applied to the head and body.

Figure 21 shows the responses of slender salamanders to a tactile stimulus applied to the body. These animals were collected in redwood forest and tested in April 1971. Tactile stimuli applied to body resulted in 43 animals (86%)

Figure 19. The direction, distance and time of movement of protean displays exhibited by slender salamanders (SVL > 33 mm) in response to a tactile stimulus applied to the dorsal surface of the tail. Number indicated at the end of the direction and distance line is the time of movement in seconds. Animals were collected in the redwood forest habitat and tested in April 1971. Symbols: n, sample size; \bar{x} , mean; SD, standard deviation \pm mean.

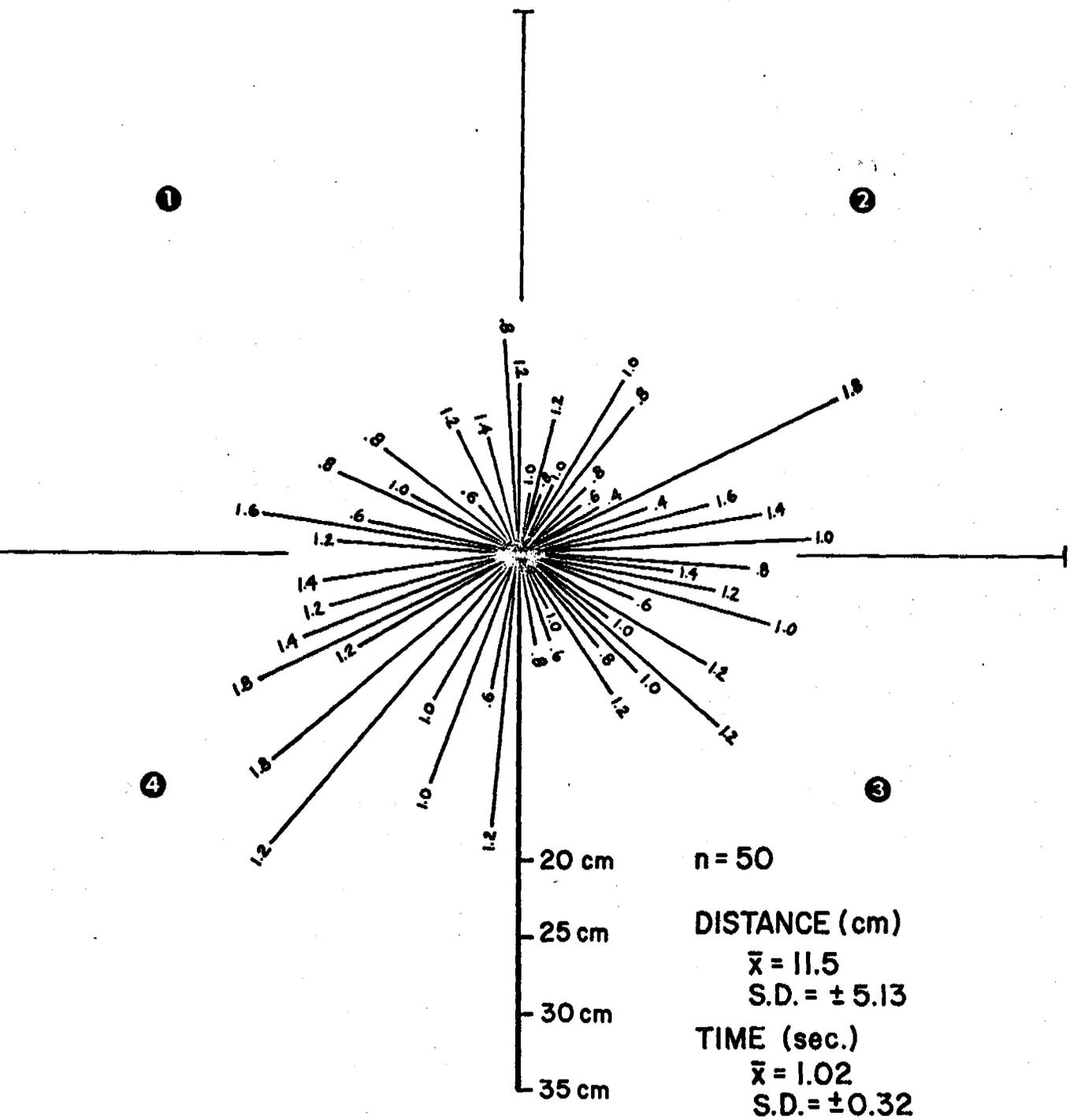
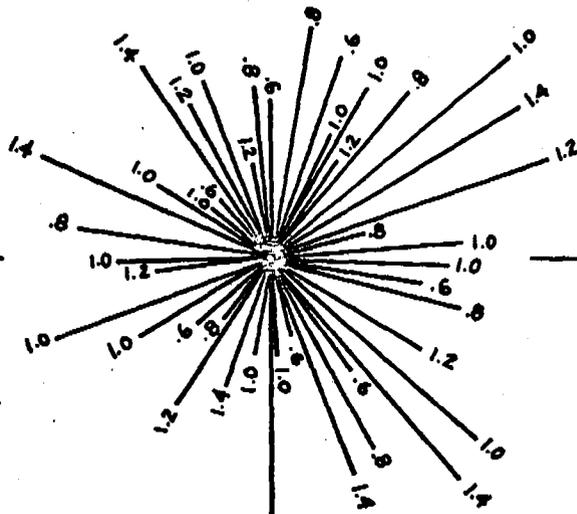


Figure 20. A comparison of the distance and time of movement of the protean displays exhibited by slender salamanders.

Figure 21. The direction, distance and time of movement of protean displays exhibited by slender salamanders (SVL > 33 mm) in response to a tactile stimulus applied to the dorsal surface of the body. Seven animals failed to respond. Number indicated at the end of the direction and distance line is the time of movement in seconds. Animals were collected in redwood forest habitat and tested in April 1971. Symbols: n, sample size; \bar{x} , mean; SD, standard deviation \pm mean.

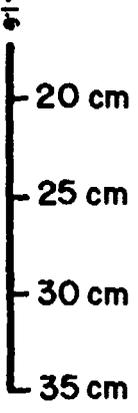
1

2



4

3



n = 50

DISTANCE (cm)

$\bar{x} = 7.96$

S.D. = ± 4.39

TIME (sec.)

$\bar{x} = .86$

S.D. = $\pm .43$

responding. Placing the dissecting pin on the dorsal surface of the body impeded the movement of 7 animals (14%). Comparison with tactile stimulation of the tail indicated that mean distance and time of movement decreased 31.3 and 15.6 percent respectively. Of those animals responding, the mean time of movement was 1.0 ± 0.26 s and mean distance was 9.2 ± 3.5 cm. Comparison of tail and body tactile stimulation for responding animals indicated no significant difference ($P > 0.05$) between the time of movement but a significant decrease ($P < 0.05$) in the distance moved when the body appears to be stimulated. Direction of movement from the stimulus contact point was random. No significant differences were noted between the expected and observed number of responses directed to quarters 1 - 4 of Figure 20 ($X^2 = 0.18$, 3 df, $P > 0.05$).

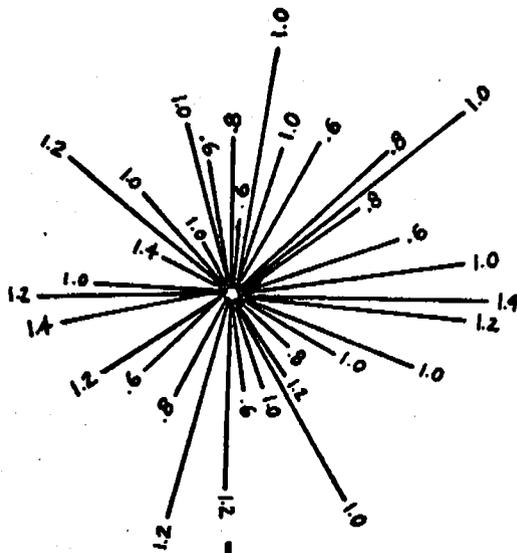
Thirty-three animals (66%) exhibited protean displays when a tactile stimulus was applied to the head (Figure 22). The non-responding animals (44%) all attempted to lower the head to the glass plate and move the head backwards quickly. Comparison with tactile stimulation of the tail indicated that mean distance and time of movement decreased 51.3 and 35.3 percent respectively. Comparisons of tail and head tactile stimulation for responding animals indicated no significant difference ($P > 0.05$) in time of movement but a significant decrease ($P < 0.05$) in the distance moved when the head was stimulated. Direction of movement from the stimulus contact point probably was also random. No significant differences were noted between the expected and observed number of responses directed to quarters 1 - 4 of Figure 21 ($X^2 = 0.31$, 3 df, $P > 0.05$).

The decrease in the mean distance and time of movement of the protean displays elicited by tactile stimulation of the head and body was caused by an experimental design bias.

Figure 22. The direction, distance and time of movement of protean displays exhibited by slender salamanders (SVL > 33 mm) in response to a tactile stimulus applied to the dorsal surface of the head. Seventeen animals failed to respond. Number at the end of direction and distance line is the time of movement in seconds. Animals were collected from the redwood forest habitat and tested in April 1971. Symbols: n, sample size; \bar{x} , mean; SD, standard deviation \pm mean.

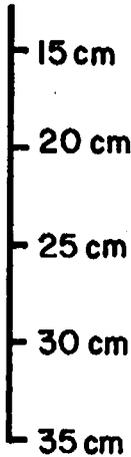
1

2



4

3



n=50

DISTANCE (cm)

$\bar{x} = 5.56$

S.D. = 4.74

TIME (sec.)

$\bar{x} = 0.66$

S.D. = 0.5

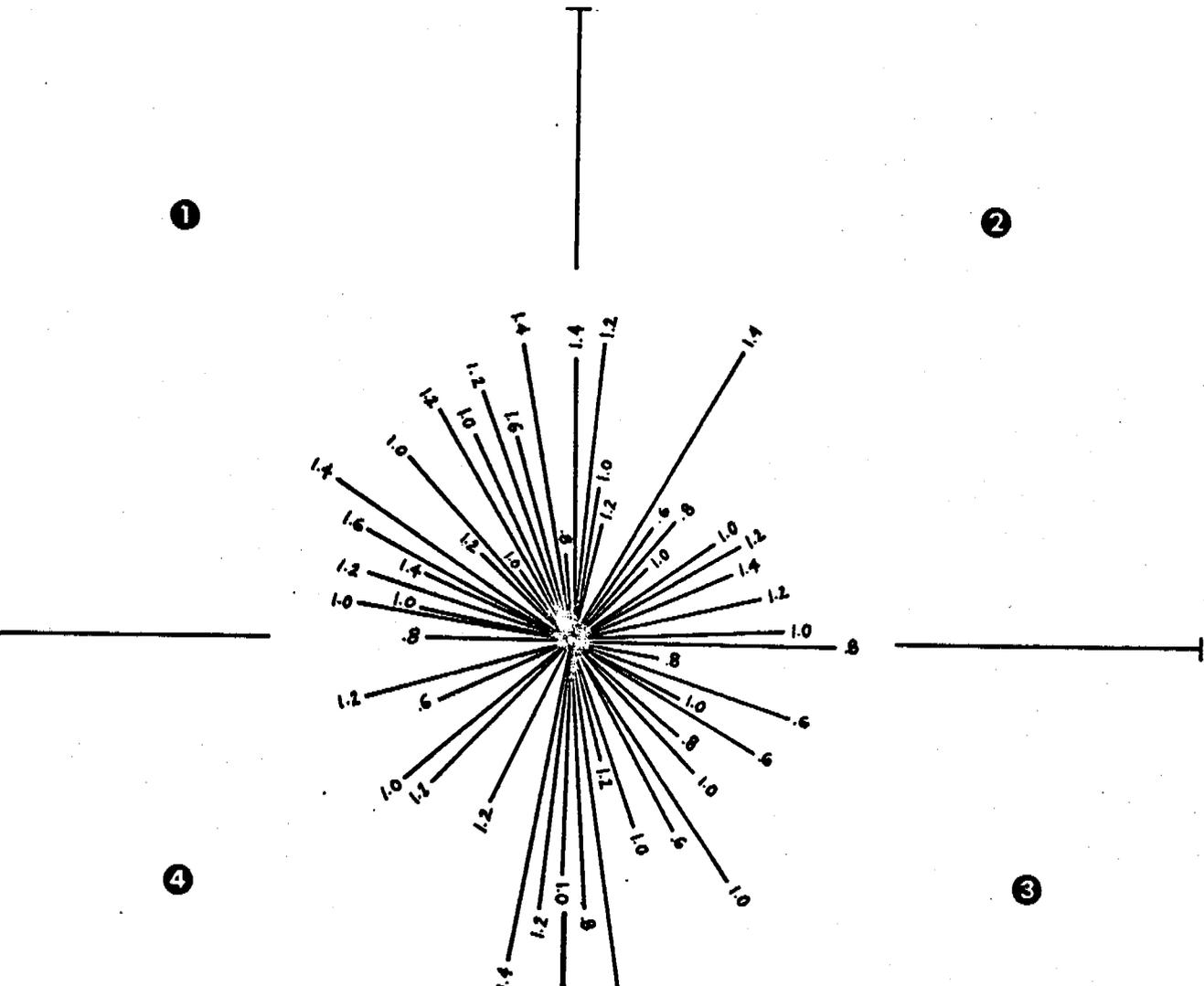
The animals could not respond to the stimulus due to the downward pressure of the dissecting pin. This source of error will be analyzed further in the discussion section, chapter V. Although the data suggest decreasing sensitivity to tactile stimulation from the tail to the head, the method of administering the stimulus was probably a significant factor in causing the apparent decreased responsiveness.

Problems associated with the application of the tactile stimuli to the body and head resulted in the discontinuance of these 2 tests. Figures 23 and 24 show the response to tactile stimulation of the tail of animals collected from edge and grassland/disturbed habitats in April 1971. Direction of movement from the contact stimulus point was apparently random. The mean distance moved was 11.5 ± 3.8 cm for edge and 11.4 ± 3.7 cm for grassland/disturbed habitats. Mean time of movement for edge habitat was 1.07 ± 0.26 s and 1.04 ± 0.26 s for grassland/disturbed habitat. Direction of movement from the stimulus contact point appeared to be random. No significant differences were noted between the observed and expected number of responses directed to quarters 1 - 4 of Figures 23 ($\chi^2 = 1.68$, 3 df, $P > 0.05$) and 24 ($\chi^2 = 2.0$, 3 df, $P > 0.05$).

Figure 25 compares the mean distance and time of movement for the protean displays elicited by a tactile stimulus applied to the tail. All habitats for April, June and August 1971 are included. No significant differences ($P < 0.05$) were found between habitats or months for the mean distance moved and the time of movement.

The similarity of protean responses between months and habitats resulted in the elimination of habitat and seasonal comparisons for the visual, olfactory and photographic analysis sections of this paper.

Figure 23. The direction, distance and time of movement of protean displays exhibited by slender salamanders (SVL > 33 mm) in response to a tactile stimulus applied to the dorsal surface of the tail. Number at end of direction and distance line is the time of movement in seconds. Animals were collected in the edge habitat and tested in April 1971. Symbols: n, sample size; \bar{x} , mean; SD, standard deviation \pm mean.



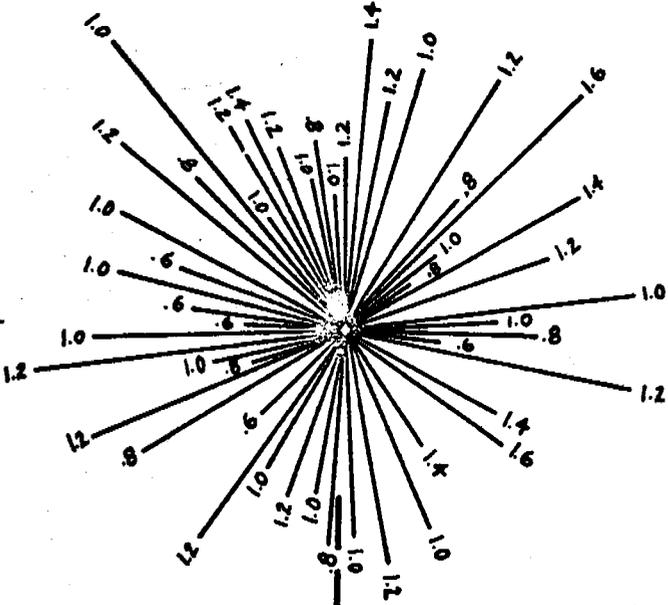
25 cm
 30 cm
 35 cm

n = 50
DISTANCE (cm)
 $\bar{x} = 11.56$
 S.D. = 3.80
TIME (sec.)
 $\bar{x} = 1.07$
 S.D. = 0.26

Figure 24. The direction, distance and time of movement of protean displays exhibited by slender salamanders (SVL > 33) in response to a tactile stimulus applied to the dorsal surface of the tail. Number at end of direction and distance line is the time of movement in seconds. Animals were collected in grassland/disturbed habitat and tested in April 1971. Symbols: n, sample size; \bar{x} , mean; SD, standard deviation \pm mean.

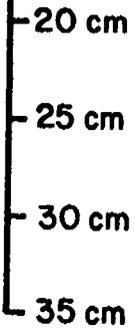
1

2



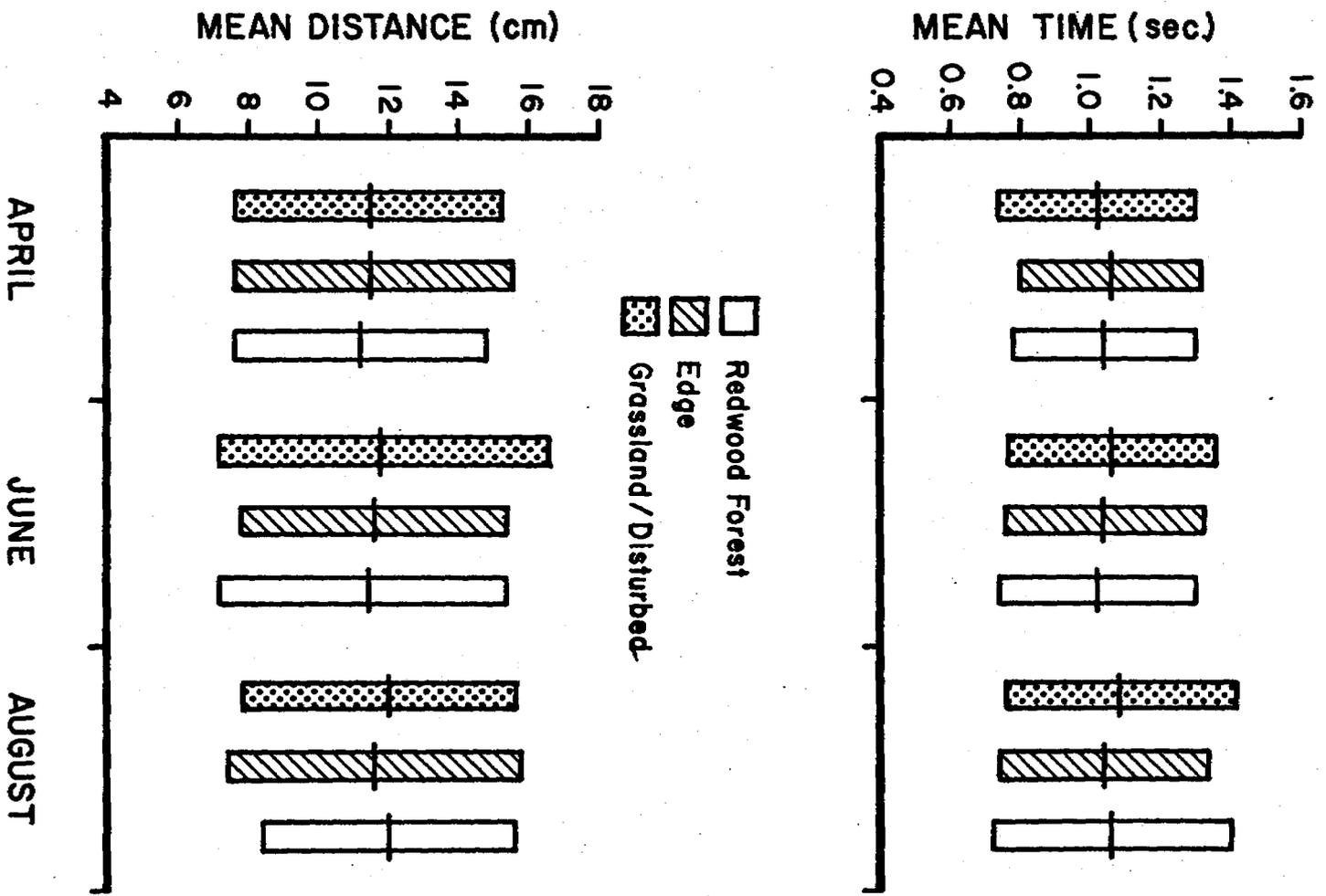
4

3



n = 50
 DISTANCE (cm)
 $\bar{x} = 11.4$
 S.D. = 3.71
 TIME (sec.)
 $\bar{x} = 1.04$
 S.D. = 0.26

Figure 25. A comparison of the mean distance and time of movement of protean displays exhibited by slender salamanders in response to a tactile stimulus applied to the dorsal surface of the tail. Animals were collected in the redwood forest, the edge and the grassland/disturbed habitats during April, June and August 1971. Sample size equals 50 for all habitats during each month. Symbols: horizontal line, mean; rectangle, standard deviation \pm mean.



Visual Response

No protean displays were exhibited by slender salamanders in response to the presentation of 20 potential vertebrate predators enclosed in clear plastic containers. No significant difference ($P > 0.05$) was observed between the control boxes and those containing predators. Of the 100 animals tested, 73 percent found shelter along the sides or in the corners of the enclosure. No protean displays or rapid movement away from the boxes containing predators were noted.

Olfactory Response

Following exposure to chemical extracts of potential predators, protean displays were exhibited only by slender salamanders with absent or regenerating tails. The tails of these animals were lost due to natural causes. Figure 26 shows the mean number of protean displays per 10 slender salamander sample which were elicited by presentation of 47 chemical extracts and 5 distilled water controls. Only salamanders with absent or regenerating tails were used for these data. A significant increase ($P < 0.05$) in the frequency of displays above those shown in the control tests was noted for these species: Pacific giant salamander, arboreal salamander, ringneck snake, common garter snake, western terrestrial garter snake and western aquatic garter snake. A significant ($P < 0.05$) increase in the mean number of protean displays per 10 animal sample was recorded for these 6 species. The single responses to the black salamander and clouded salamander were probably the result of inadvertently touching the animals with the glass pipette.

Figure 27 is a comparison of the mean distance and time of movement of the protean displays exhibited by slender salamanders in response to tactile stimulation of the tail, with and without prior exposure to the chemical extracts of

Figure 26. A comparison of the mean number of protean displays exhibited by slender salamanders (SVL > 33 mm) with absent or regenerating tails in response to chemical extracts of potential predator species. Ten slender salamanders were tested with a chemical extract derived from each predator. Symbols: n, total number of slender salamanders tested.

CHEMICAL EXTRACT

MEAN NUMBER OF
PROTEAN DISPLAYS

1 2 3 4 5 6 7 8 9 10

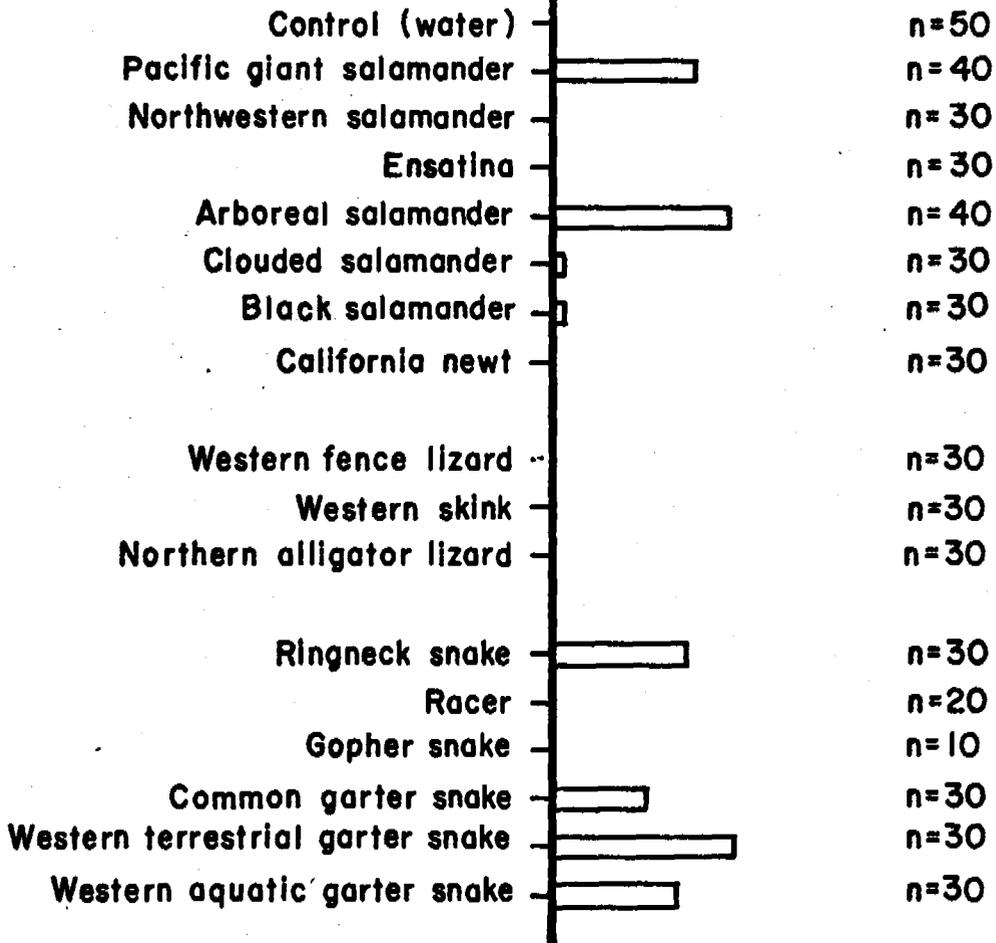
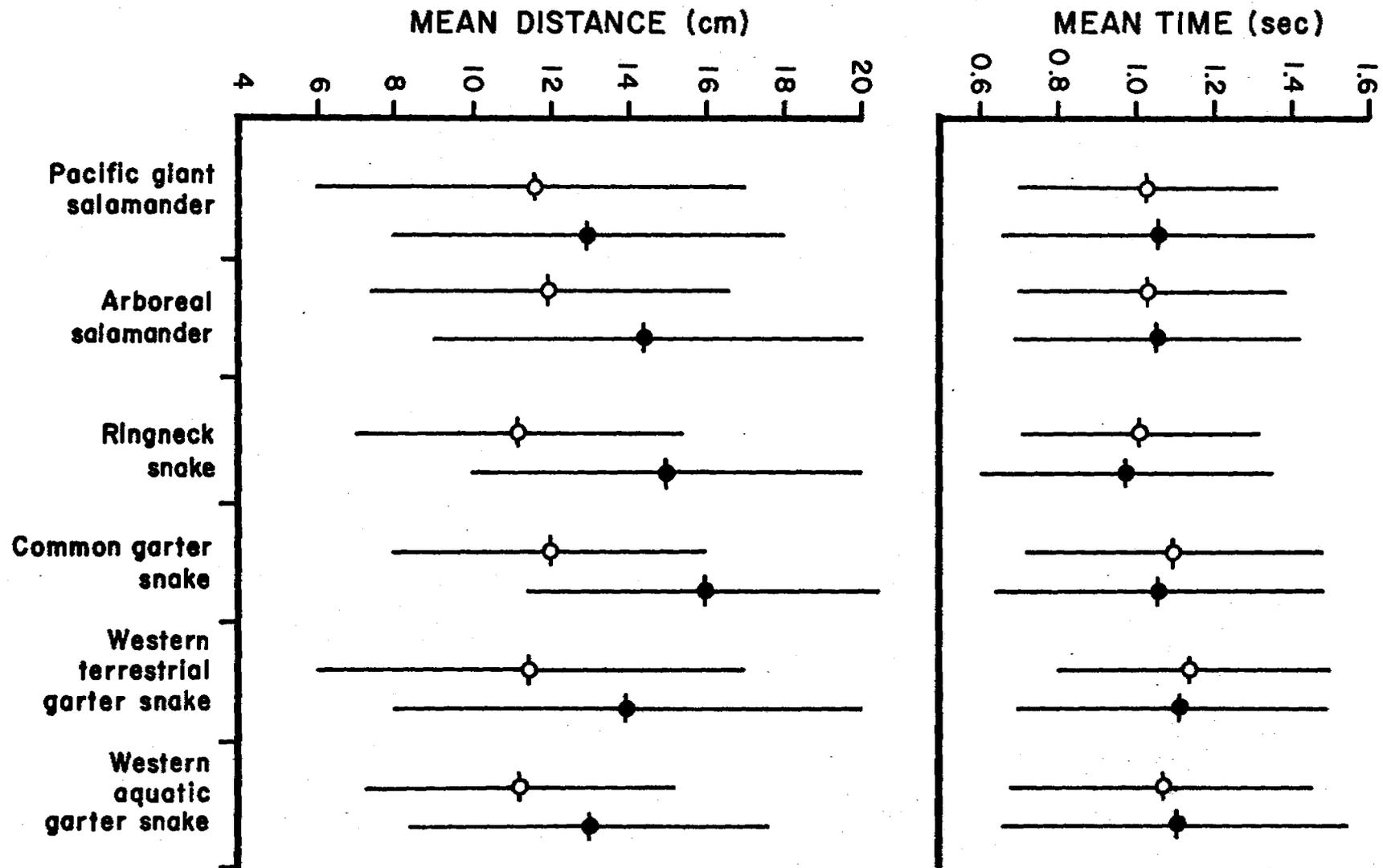


Figure 27. A comparison of the mean distance and time of movement of protean displays exhibited by slender salamanders (SVL > 33 mm) in response to a tactile and olfactory/tactile stimulus. Symbols: horizontal line, mean; vertical line, standard deviation \pm mean; -O-, tactile stimulus; -●-, olfactory/tactile stimulus.



predators. The extracts used were those which elicited a significant number of protean displays (Figure 26). No significant differences ($P > 0.05$) between the control (tactile stimulus) and experimental (extract/tactile stimulus) groups were noted for time of movement. Distance of movement in the experimental group increased significantly ($P < 0.05$) for all extracts tested. For all species the increase in mean distance moved was 22.5 ± 9.3 percent. No differences were noted between the response of animals with complete or regenerating tails. Comparison of linear regression analyses of duration of movement and distance moved for the tactile and combined tactile/olfactory stimuli showed an increase in the correlation coefficient for tactile/olfactory stimuli ($r^2 = 0.385$, $P > 0.05$). This comparison suggests a more linear relationship for the olfactory/tactile response.

Photographic Analysis

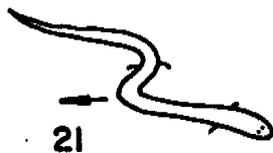
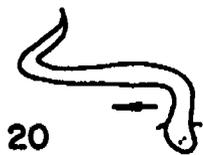
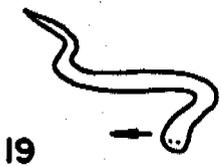
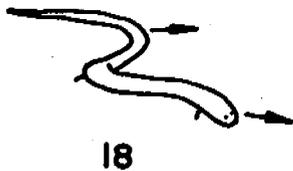
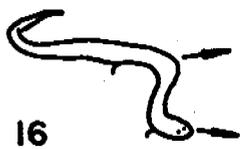
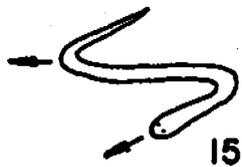
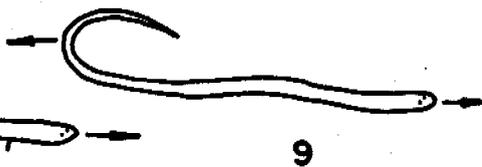
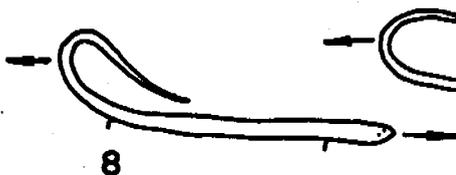
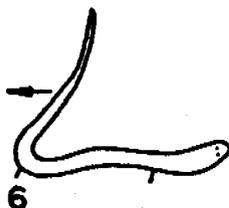
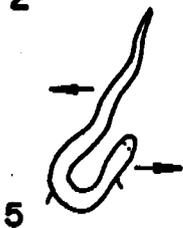
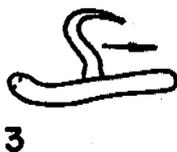
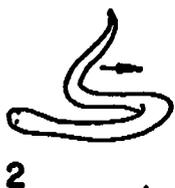
Table 6 summarizes the predator escape responses of slender salamanders elicited by an electric shock applied to the head, body or tail region. Three characteristic responses to the shock were observed: 1) body avoidance, 2) serpentine movement, and 3) protean display. The avoidance response consisted of a short rapid movement of the shocked body part away from the probe. Serpentine movement consisted of exaggerated snake-like movement which took the salamander from 3 to 15 cm from the probe. The protean display involved violent and erratic flipping movements lasting for less than 2 seconds and taking the salamander from 5 to 35 cm from the probe. Figures 28 and 29 depict the sequential action of characteristic serpentine movement and protean displays. The sequence started with electrical stimulus contact with the test animal and ended when the rapid movement stopped.

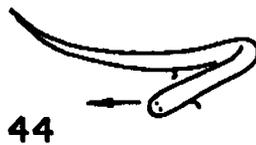
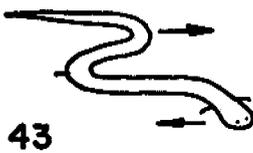
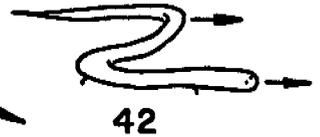
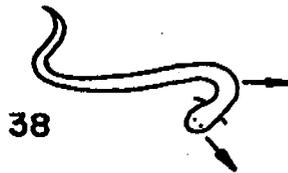
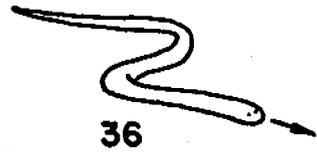
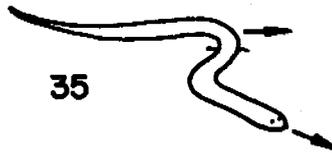
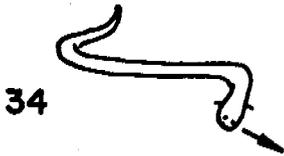
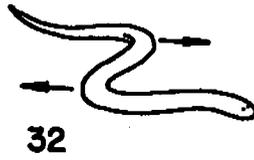
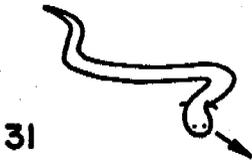
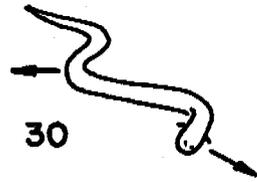
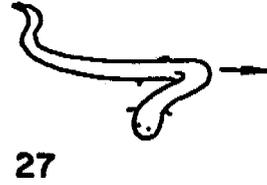
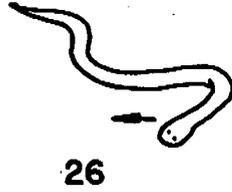
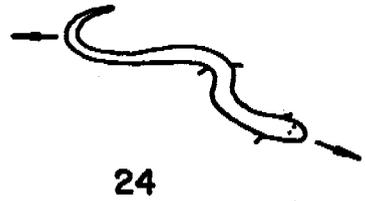
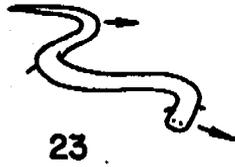
Table 6. A summary of the behavioral responses of slender salamanders (SVL > 33 mm) to an electric shock (25 volt, 0.4 amp.) applied to the head, body and tail region. Symbols: N, number of test animals.

Body Area Shocked	N	Behavioral Responses					
		Body Avoidance	(%)	Serpentine Movement	(%)	Protean Display	(%)
Tail	25	9	(36.0)	10	(40.0)	6	(24.0)
Body	25	7	(28.0)	9	(36.0)	9	(36.0)
Head	25	10	(40.0)	1	(4.0)	14	(56.0)
	Totals	26		20		29	

Figure 28. A 1.35 second sequence of characteristic serpentine movement elicited by an electrical stimulus (25 volt, 0.4 amp.). Each sequence represents a 0.03 second interval. Direction of head and tail movement and use of limbs is indicated in each frame.

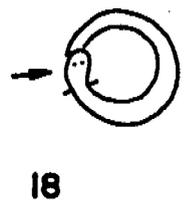
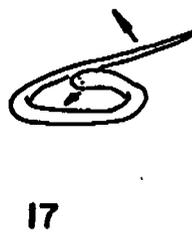
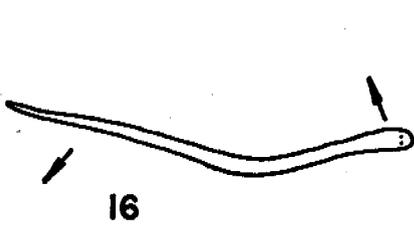
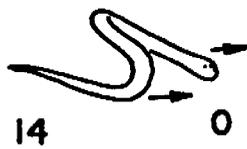
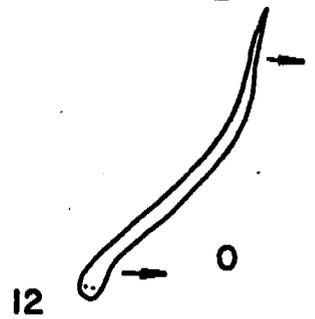
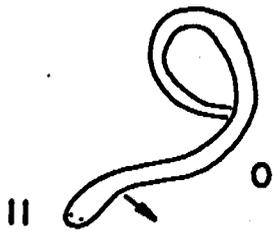
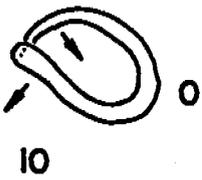
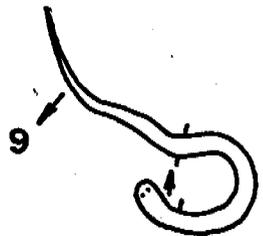
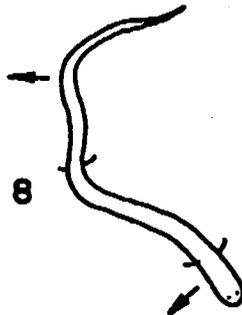
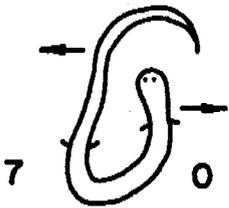
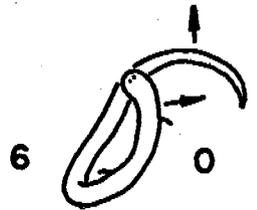
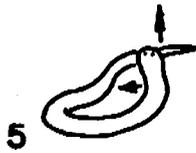
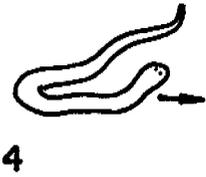
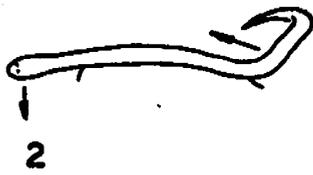
STIMULUS
CONTACT

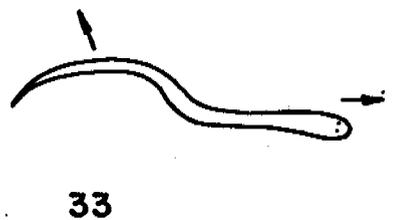
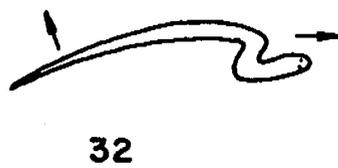
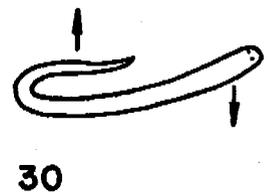
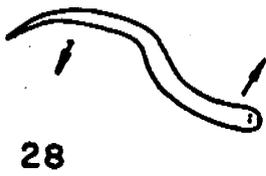
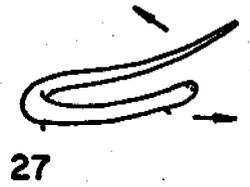
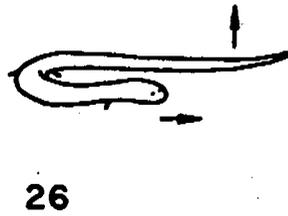
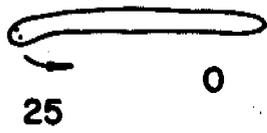
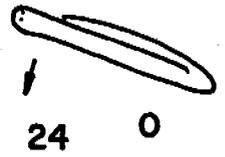
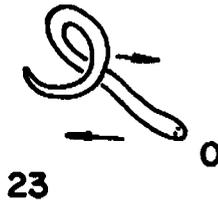
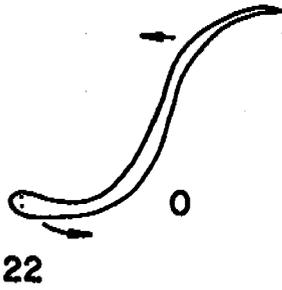
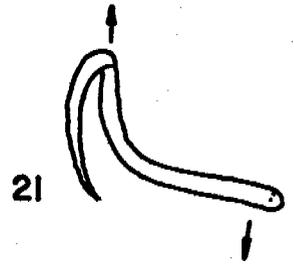
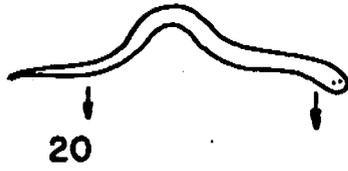


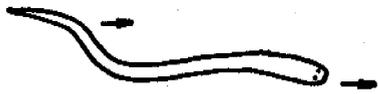


AT REST

Figure 29. A 1.17 second sequence of characteristic protean display elicited by an electrical stimulus (25 volt, 0.4 amp.). Each figure represents a 0.03 second interval. Direction of head and tail movement and the use of limbs is indicated for each frame. Symbols: O, animal not in contact with substrate.







34



35



36



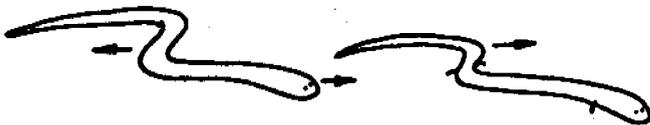
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38



39



40



41



42

AT REST

The avoidance response appeared to be a response to pain and an attempt to withdraw the affected body part. No other body movement or response was associated with this response. The variability of serpentine movement and protean displays did not allow for precise categorization of these responses. However, basic components of these responses were similar. The serpentine movement was always directed away from the stimulus. The movement consisted of the following components: 1) tail movements (Figure 28, sequences 1 - 9), 2) serpentine movement without the use of limbs (Figure 28, sequences 10 - 15) and 3) serpentine movement with intermittent use of limbs (Figure 28, sequences 16 - 30).

The protean display was much more variable in terms of movement components. No identifiable pattern of head or tail movement associated with shocking a particular body part was discerned from viewing the displays at a speed of 1 frame per second. However, some generalization can be made regarding the nature of the movement. At some point during all displays the body was thrown into the air and was not in contact with the glass plate. Of the 29 protean displays observed, animals lost contact with the glass substrate from 1 to 6 times and averaged 3.3 ± 1.7 times. The simultaneous pushing of the head and tail against the glass plate combined with a violent body contraction resulted in the animal being thrown into the air (Figure 29, sequences 5-6, 13-14, 17-18). The display ended in either serpentine movement (Figure 29, sequences 29 - 39) or the animal appeared to "freeze" after coming to rest. Of the 29 protean displays 48.3 percent ended with the "freeze" response and 51.7 percent with serpentine movement. Due to the variability of the protean display and the difficulty in quantifying the components of the movement, a 16-mm film depicting

various protean displays has been placed on file with the Humboldt State University library. This film should be viewed at a speed of 1 frame per second to observe all components of this behavior.

Table 6 suggests increased sensitivity to electrical stimulus from the tail to the head area. The number of protean displays increased 50 percent with body stimulation and 133 percent with head stimulation. Body avoidance remained relatively constant regardless of the body part shocked. An inverse relationship appears to exist between serpentine movement and protean displays in relation to the body part shocked. Moving from the tail to the head, the number of serpentine responses decreased as the number of protean displays increased.

Prey Palatability and Toxicity

The responses of 22 species of vertebrates to force feeding of tail and body sections of slender salamanders is summarized in Table 7. No mortality occurred due to force feeding. No difference in the responses to tail or body sections was noted. Salamanders, whose normal diet was insects, slugs and worms (Stebbins 1954, 1972), tended to regurgitate the sections immediately or within a few hours. Lizards usually refused to swallow the sections or regurgitated immediately. Western fence lizards showed decreased activity after force feeding. Inactivity following force feeding was usually due to the trauma associated with force feeding. Force feeding with preferred food items confirmed this observation. Snakes either voluntarily ingested or accepted sections with little difficulty and few reactions.

With the exception of the Townsend mole, all mammals refused to swallow and were orally force fed with a water skin solution through a blunt needle. Reaction to this

Table 7. Summary of the responses to force feeding of 30-mm tail or body sections of slender salamanders to potential vertebrate predators. Symbols: SVL, snout vent length; WT, weight; N, number of force feedings.

Predator Species	SVL (cm)	TL (cm)	WT (g)	N	Response		Remarks
					Regurgi- tated	Ingested	
Pacific giant salamander	12.7	--	--	10	0	10	
	11.4	--	--	10	0	10	
	12.0	--	--	10	0	10	
	11.0	--	--	10	0	10	
Northwestern salamander	8.8	--	--	10	4	6	regurgitated 3 sections after 2-8 hrs.
	8.0	--	--	10	2	8	
	9.1	--	--	10	5	5	regurgitated 2 sections after 6 hrs.
Ensatina	6.3	--	--	10	8	2	regurgitated 1 section after 4 hrs.
	6.0	--	--	10	9	1	
	6.6	--	--	10	7	1	
Arboreal salamander	6.3	--	--	10	0	10	
	7.6	--	--	10	0	10	
	7.1	--	--	10	0	10	
	7.3	--	--	10	0	10	
Clouded salamander	5.0	--	--	5	4	1	regurgitated all 4 sections immediately
	6.1	--	--	5	3	2	regurgitated immediately
	7.4	--	--	5	5	0	regurgitated after 6 hrs.
Black salamander	6.3	--	--	5	3	2	immediate regurgitation
	6.7	--	--	5	5	0	immediate regurgitation
	7.1	--	--	5	5	0	immediate regurgitation
Rough-skinned newt	6.3	--	--	5	5	0	immediate regurgitation
	6.7	--	--	5	4	1	immediate regurgitation
	6.9	--	--	5	2	3	regurgitated 2 sections after 6 hrs.
Western fence lizard	6.1	--	--	5	4	1	reduced activity for 24 hrs.
	6.8	--	--	5	3	2	reduced activity for 12-24 hrs.
	7.3	--	--	5	4	1	reduced activity for 72 hrs.

Western skink	6.0	--	--	5	5	0	immediate regurgitation
	6.4	--	--	5	5	0	immediate regurgitation
	7.1	--	--	5	3	2	
Northern alligator lizard	10.1	--	--	5	3	2	regurgitated immediately
	13.3	--	--	5	2	3	
	14.0	--	--	5	4	1	regurgitated immediately
Ringneck snake	--	35.5	--	10	0	10	
	--	40.5	--	10	0	10	
	--	50.9	--	10	0	10	
Racer	--	66.0	--	10	0	10	occasional inactivity after feeding
	--	63.0	--	10	0	10	
Gopher snake	--	83.8	--	10	1	9	regurgitated after 1 hr.
Common garter snake	--	48.2	--	10	0	10	
	--	66.1	--	10	0	10	
	--	75.3	--	10	0	10	
Western terrestrial garter snake	--	46.2	--	10	0	10	
	--	55.8	--	10	0	10	
	--	69.3	--	10	0	10	
Western aquatic garter snake	--	49.3	--	10	0	10	
	--	52.6	--	10	1	9	regurgitated 1 section immediately
	--	73.4	--	10	0	10	
Townsend mole	--	--	120.3	5	0	5	
	--	--	128.1	5	0	5	
Vagrant shrew	--	--	6.7	5	3	2	regurgitated 2 sections
	--	--	7.1	5	2	3	regurgitated 2 sections
	--	--	7.2	5	1	4	no regurgitation
Dusky-footed woodrat	--	--	255.3	5	1	4	regurgitated immediately
	--	--	298.1	5	2	3	regurgitated 1 section
Norway rat	--	--	199.0	5	4	1	regurgitated immediately
	--	--	215.1	5	5	0	regurgitated immediately
	--	--	232.1	5	5	0	regurgitated immediately
Black rat	--	--	155.6	5	5	0	regurgitated immediately

Deer mouse *	--	--	22.3	5	4	1	regurgitated - inactivity
	--	--	24.1	5	5	0	regurgitated
	--	--	25.6	5	3	2	inactivity
	--	--	28.6	5	2	3	inactivity
	--	--	30.3	5	3	2	regurgitated

* fed 10 mm sections due to small body size.

feeding was either immediate regurgitation or decreased activity for a 24 - 48 hour period after ingestion. Both moles fed upon slender salamanders as a normal food item during their 1-month captivity. This observation corresponds to the reactions of the California mole (Scapanus latimanus) reported by Anderson (1963).

With 1 exception, species which tended to regurgitate or refuse to swallow slender salamanders did not react in this manner when offered preferred food items. Preferred food items consisted of insects for insectivorous salamanders, lizards and shrews, grain and peanut butter for rodents.

Tail Autotomy

The number of minutes in which tails moved following mechanical severing is shown in Figure 30. Tail movement was recorded from the time of severing until the tail showed no significant movement. No significant difference ($P > 0.05$) occurred between habitat types. Samples from redwood forest and grassland/disturbed habitats were tested at 11.1° C and the edge sample at 15.5° C. The increased temperature for the edge sample may have accounted for the slight increase in mean number of minutes moved.

Following severing of the tail, slender salamanders exhibited these types of behavioral responses: 1) no movement, 2) serpentine movement, and 3) protean displays. Table 8 indicates the percent of behavioral responses noted for the 3 habitat types. No significant differences were noted between habitat types. The no-movement response consisted of slow movement for 1 to 4 cm followed by no movement for 30 to 90 seconds. Serpentine movement consisted of lateral undulations away from the point at which the tail was severed. Protean displays occurred in a similar manner as described for the response to tactile stimuli.

Figure 30. A comparison of the mean number of minutes moved by severed tails of slender salamanders (SVL > 33 mm) collected in 3 habitat types during April 1971.

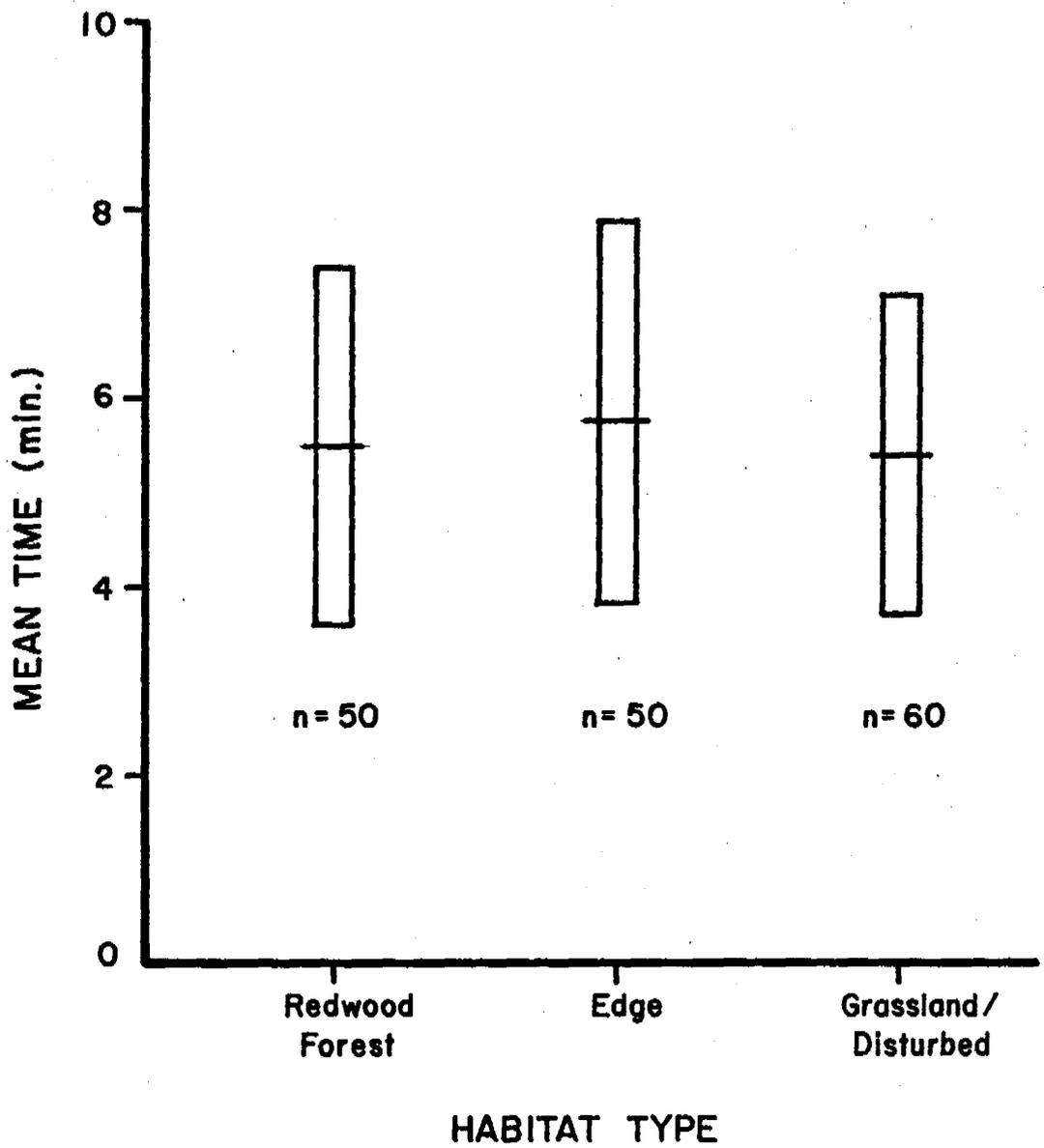


Table 8. A comparison of the number of behavioral responses exhibited by slender salamanders following mechanical severing of the tail.

Response	Habitat Type					
	Redwood Forest	(%)	Edge	(%)	Grassland/ Disturbed	(%)
No movement	15	(30.0)	13	(26.0)	16	(26.7)
Serpentine movement	15	(30.0)	14	(28.0)	19	(31.7)
Protean display	20	(40.0)	23	(46.0)	25	(41.6)
Totals	50	(100.0)	50	(100.0)	60	(100.0)

Predator-Prey Interactions

The responses exhibited by slender salamanders to attacks by captive predators are summarized in Tables 9, 10, 11 and 12. Successful attacks were defined as those in which the predator captured and ingested the entire salamander. Unsuccessful attacks consisted of those in which the entire salamander escaped or the tail was autotomized during an attack resulting in the salamander's escape. Due to the speed of many of the attacks it was not usually possible to differentiate between a head or body attack, however, head/body versus tail attacks could be distinguished. The percentage of attacks made to the head/body versus tail area are equivalent to successful (head/body) and unsuccessful (tail) attacks as shown in Table 9. A detailed account of predator-prey interactions by predator species has been included to clarify the variability of the responses of individuals of the same species. In the following sections, slender salamanders will be referred to as the prey and each potential predator as the predator. Unless otherwise indicated percentages are expressed as averages.

Pacific Giant Salamander: In all attacks this predator slowly approached the prey and then quickly attacked. This predator attacked 58.0 percent of the prey presented to it. Of the total attacks made 52.4 percent were successful. All successful attacks involved seizing the head or body of the prey. The prey exhibited protean behavior in 22.9 percent of successful attacks and 91.7 percent of unsuccessful attacks. Tail autotomy occurred only during unsuccessful attacks. Following tail autotomy, 83.3 percent of the tails were ingested. Only during a single attack did this predator pursue the prey following tail autotomy.

Table 9. The number of successful and unsuccessful attacks made by potential vertebrate predators on slender salamanders (SVL > 33 mm). Symbols: \bar{x} , mean; N, number of slender salamanders tested.

Predator Species	N	Number of Attacks					
		Total	(%)	Successful	(%)	Unsuccessful	(%)
Pacific giant salamander	10	6	(60.0)	4	(66.7)	2	(33.3)
	10	7	(70.0)	3	(42.9)	4	(57.1)
	10	4	(40.0)	2	(50.0)	2	(50.0)
	10	6	(60.0)	3	(50.0)	3	(50.0)
	\bar{x}		5.8	(58.0)	3.0	(52.4)	2.8
Arboreal salamander	10	6	(60.0)	3	(50.0)	3	(50.0)
	10	4	(40.0)	3	(75.0)	1	(25.0)
	10	7	(70.0)	4	(57.1)	3	(42.9)
	10	3	(30.0)	2	(66.7)	1	(33.3)
	\bar{x}		5.0	(50.0)	3.0	(62.2)	2.0
Ringneck snake	10	7	(70.0)	4	(57.1)	3	(42.9)
	10	7	(70.0)	3	(42.9)	4	(57.1)
	10	5	(50.0)	3	(60.0)	2	(40.0)
	\bar{x}		6.3	(63.3)	3.3	(53.3)	3.0
Racer	10	2	(20.0)	2	(100.0)	0	(0.0)
	10	0	(0.0)	0	(0.0)	0	(0.0)
	\bar{x}		1.0	(10.0)	1.0	(50.0)	0.0
Common garter snake	10	3	(30.0)	2	(66.7)	1	(33.3)
	10	5	(50.0)	5	(100.0)	0	(0.0)
	10	2	(20.0)	1	(50.0)	1	(50.0)
	\bar{x}		3.3	(33.3)	2.7	(72.2)	0.7
Western terrestrial garter snake	10	4	(40.0)	2	(50.0)	2	(50.0)
	10	5	(50.0)	4	(80.0)	1	(20.0)
	10	3	(30.0)	1	(33.3)	2	(66.7)
	\bar{x}		4.0	(40.0)	2.6	(54.4)	1.7
Western aquatic garter snake	10	4	(40.0)	2	(50.0)	2	(50.0)
	10	3	(30.0)	2	(66.7)	1	(33.3)
	10	6	(60.0)	5	(83.3)	1	(16.7)
	\bar{x}		4.3	(43.3)	3.0	(66.7)	1.3
Townsend mole	10	10	(100.0)	10	(100.0)	0	(0.0)
	10	10	(100.0)	10	(100.0)	0	(0.0)
	\bar{x}		10.0	(100.0)	10.0	(100.0)	0.0

Vagrant shrew	10	1	(10.0)	0	(0.0)	1	(100.0)
	10	1	(10.0)	0	(0.0)	1	(100.0)
	10	0	(0.0)	0	(0.0)	0	(0.0)
	\bar{X}	0.7	(0.7)	0.0	(0.0)	0.7	(66.7)
Dusky-footed woodrat	10	1	(10.0)	0	(0.0)	1	(100.0)
	10	1	(10.0)	0	(0.0)	1	(100.0)
	\bar{X}	1.0	(10.0)	0.0	(0.0)	1.0	(100.0)
Norway rat	10	2	(20.0)	0	(0.0)	2	(100.0)
	10	1	(10.0)	0	(0.0)	1	(100.0)
	10	1	(10.0)	0	(0.0)	1	(100.0)
	\bar{X}	1.3	(13.3)	0.0	(0.0)	1.3	(100.0)
Black rat	10	1	(10.0)	0	(0.0)	1	(100.0)
Northwestern salamander	30	0	(0.0)	0	(0.0)	0	(0.0)
Ensatina	30	0	(0.0)	0	(0.0)	0	(0.0)
Clouded salamander	30	0	(0.0)	0	(0.0)	0	(0.0)
Black salamander	30	0	(0.0)	0	(0.0)	0	(0.0)
Rough-skinned newt	30	0	(0.0)	0	(0.0)	0	(0.0)
Western fence lizard	30	0	(0.0)	0	(0.0)	0	(0.0)
Western skink	30	0	(0.0)	0	(0.0)	0	(0.0)
Northern alligator lizard	30	0	(0.0)	0	(0.0)	0	(0.0)
Gopher snake	10	0	(0.0)	0	(0.0)	0	(0.0)
Deer mouse	50	0	(0.0)	0	(0.0)	0	(0.0)

Table 10. The number of protean displays exhibited by slender salamanders (SVL > 33 mm) during successful and unsuccessful attacks made by vertebrate predators. Symbols: \bar{x} , mean.

Predator Species	Total Attacks	Successful Attacks		Unsuccessful Attacks	
		No. of Attacks	Protean Displays (%)	No. of Attacks	Protean Displays (%)
Pacific giant salamander	6	4	1 (25.0)	2	2 (100.0)
	7	3	0 (0.0)	4	4 (100.0)
	4	2	0 (0.0)	2	2 (100.0)
	6	3	2 (66.7)	3	2 (66.7)
	\bar{x}	5.8	3.0	0.8 (22.9)	2.8
Arboreal salamander	6	3	0 (0.0)	3	3 (100.0)
	4	3	0 (0.0)	1	1 (100.0)
	7	4	1 (25.0)	3	2 (66.7)
	3	2	1 (50.0)	1	1 (100.0)
	\bar{x}	5.0	3.0	0.5 (18.8)	2.0
Ringneck snake	7	4	1 (25.0)	3	3 (100.0)
	7	3	0 (0.0)	4	4 (100.0)
	5	3	0 (0.0)	2	1 (50.0)
	\bar{x}	6.3	3.3	0.3 (8.3)	3.0
Racer	2	2	0 (0.0)	0	0 (0.0)
	0	0	0 (0.0)	0	0 (0.0)
	\bar{x}	1.0	1.0	0.0 (0.0)	0.0
Common garter snake	3	2	0 (0.0)	1	1 (100.0)
	5	5	0 (0.0)	0	0 (100.0)
	2	1	0 (0.0)	1	1 (100.0)
	\bar{x}	3.3	2.7	0.0 (0.0)	0.7
Western terrestrial garter snake	4	2	0 (0.0)	2	2 (100.0)
	5	4	1 (25.0)	1	1 (100.0)
	3	1	0 (0.0)	2	2 (100.0)
	\bar{x}	4.0	2.6	0.3 (8.3)	1.7
Western aquatic garter snake	4	2	0 (0.0)	2	2 (100.0)
	3	2	0 (0.0)	1	1 (100.0)
	6	5	1 (20.0)	1	1 (100.0)
	\bar{x}	4.3	3.0	0.3 (6.7)	1.3
Townsend mole	10	10	0 (0.0)	0	0 (0.0)
	10	10	0 (0.0)	0	0 (0.0)
	\bar{x}	10.0	10.0	0.0 (0.0)	0.0

Vagrant shrew		1	0	0	(0.0)	1	0	(0.0)
		1	0	0	(0.0)	01	0	(0.0)
		0	0	0	(0.0)	0	0	(0.0)
	\bar{x}	0.7	0.0	0.0	(0.0)	0.7	0.0	(0.0)
Dusky-footed woodrat		1	0	0	(0.0)	1	1	(100.0)
		1	0	0	(0.0)	1	1	(100.0)
	\bar{x}	1.0	0.0	0.0	(0.0)	1.0	1.0	(100.0)
Norway rat		2	0	0	(0.0)	2	0	(0.0)
		1	0	0	(0.0)	1	0	(0.0)
		1	0	0	(0.0)	1	0	(0.0)
	\bar{x}	1.3	0.0	0.0	(0.0)	1.3	0.0	(0.0)
Black rat		1	0	0	(0.0)	1	0	(0.0)

Table 11. The number of tails autotomized by slender salamanders (SVL > 33 mm) during successful and unsuccessful attacks by vertebrate predators. Symbols: \bar{x} , mean.

Predator Species	Total Attacks	Successful Attacks			Unsuccessful Attacks		
		No. of Attacks	No. of Tails Autotomized	(%)	No. of Attacks	No. of Tails Autotomized	(%)
Pacific giant salamander	6	4	0	(0.0)	2	1	(50.0)
	7	3	0	(0.0)	4	2	(30.0)
	4	2	0	(0.0)	2	2	(100.0)
	6	3	0	(0.0)	3	1	(33.3)
	\bar{x}	5.8	3.0	0.0	(0.0)	2.8	1.5
Arboreal salamander	6	3	0	(0.0)	3	2	(66.7)
	4	3	0	(0.0)	1	1	(100.0)
	7	4	0	(0.0)	3	0	(0.0)
	3	2	0	(0.0)	1	1	(100.0)
	\bar{x}	5.0	3.0	0.0	(0.0)	2.0	1.0
Ringneck snake	7	4	0	(0.0)	3	2	(66.7)
	7	3	0	(0.0)	4	3	(75.0)
	5	3	0	(0.0)	2	1	(50.0)
	\bar{x}	6.3	3.3	0.0	(0.0)	3.0	2.0
Racer	2	2	0	(0.0)	0	0	(0.0)
	0	0	0	(0.0)	0	0	(0.0)
	\bar{x}	1.0	1.0	0	(0.0)	0.0	0.0
Common garter snake	3	2	0	(0.0)	1	1	(100.0)
	5	5	1	(20.0)	0	0	(0.0)
	2	1	0	(0.0)	1	1	(100.0)
	\bar{x}	3.3	2.7	0.3	(11.1)	0.7	0.7
Western terrestrial garter snake	4	2	0	(0.0)	2	2	(100.0)
	5	4	0	(0.0)	1	1	(100.0)
	3	1	0	(0.0)	2	1	(50.0)
	\bar{x}	4.0	2.6	0.0	(0.0)	1.7	1.3
Western aquatic garter snake	4	2	0	(0.0)	2	1	(50.0)
	3	2	0	(0.0)	1	0	(0.0)
	6	5	0	(0.0)	1	1	(100.0)
	\bar{x}	4.3	3.0	0.0	(0.0)	1.3	0.7
Townsend mole	10	10	0	(0.0)	0	0	(0.0)
	10	10	0	(0.0)	0	0	(0.0)
	\bar{x}	10.0	10.0	0.0	(0.0)	0.0	0.0

Vagrant shrew		1	0	0	(0.0)	1	0	(0.0)
		1	0	0	(0.0)	1	0	(0.0)
		0	0	0	(0.0)	0	0	(0.0)
	\bar{x}	0.7	0.0	0.0	(0.0)	0.7	0.0	(0.0)
Dusky-footed woodrat		1	0	0	(0.0)	1	0	(0.0)
		1	0	1	(0.0)	1	0	(0.0)
	\bar{x}	1.0	0.0	0.0	(0.0)	1.0	0.0	(0.0)
Norway rat		2	0	0	(0.0)	2	0	(0.0)
		1	0	0	(0.0)	1	0	(0.0)
		1	0	0	(0.0)	1	0	(0.0)
	\bar{x}	1.3	0.0	0.0	(0.0)	1.3	0.0	(0.0)
Black rat		1	0	0	(0.0)	1	0	(0.0)

Table 12. The responses of vertebrate predators to tail autotomy by slender salamanders (SVL > 33 mm) occurring during an attack. Ten salamanders were tested for each predator. Symbols: N, number of attacks; N¹, number of tails autotomized during attacks; \bar{x} , mean.

Predator Species	N	N ¹	(%)	Responses					
				Ingested Tail (%)	Pursued Prey (%)	Discontinued Attack (%)			
Pacific giant salamander	6	1	(16.7)	1	(100.0)	0	(0.0)	0	(0.0)
	7	2	(28.6)	1	(50.0)	1	(50.0)	0	(0.0)
	4	2	(50.0)	2	(100.0)	0	(0.0)	0	(0.0)
	6	1	(16.7)	1	(100.0)	0	(0.0)	0	(0.0)
	\bar{x}	5.8	1.5	(25.9)	1.3	(83.3)	0.3	(16.7)	0.0
Arboreal salamander	6	2	(33.3)	1	(50.0)	0	(0.0)	1	(50.0)
	4	1	(25.0)	1	(100.0)	0	(0.0)	0	(0.0)
	7	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)
	3	1	(33.3)	1	(100.0)	0	(0.0)	0	(0.0)
	\bar{x}	5.0	1.0	(20.0)	0.8	(75.0)	0.0	(0.0)	0.3
Ringneck snake	7	2	(28.5)	1	(50.0)	1	(50.0)	0	(0.0)
	7	3	(42.9)	2	(66.7)	0	(0.0)	1	(33.3)
	5	1	(20.0)	1	(100.0)	0	(0.0)	0	(0.0)
	\bar{x}	6.3	2.0	(31.7)	1.3	(66.5)	0.3	(16.5)	0.3
Common garter snake	3	1	(33.3)	1	(100.0)	0	(0.0)	0	(0.0)
	5	1	(20.0)	1	(100.0)	0	(0.0)	0	(0.0)
	2	1	(50.0)	0	(0.0)	0	(0.0)	1	(100.0)
	\bar{x}	3.3	1.0	(30.3)	0.7	(67.3)	0.0	(0.0)	0.3
Western terrestrial garter snake	4	2	(50.0)	2	(100.0)	0	(0.0)	0	(0.0)
	5	1	(20.0)	1	(100.0)	0	(0.0)	0	(0.0)
	3	1	(33.3)	1	(100.0)	0	(0.0)	0	(0.0)
	\bar{x}	4.0	1.3	(32.5)	1.3	(100.0)	0.0	(0.0)	0.0
Western aquatic garter snake	4	1	(20.0)	1	(100.0)	0	(0.0)	0	(0.0)
	3	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)
	6	1	(16.7)	1	(100.0)	0	(0.0)	0	(0.0)
	\bar{x}	4.3	0.7	(15.6)	0.7	(100.0)	0.0	(0.0)	0.0

Northwestern Salamander: No attacks were initiated by this predator. Both predator and prey tended to remain along the edge of the enclosure attempting to find cover.

Ensatina: No attacks were initiated by this predator and both predator and prey sought cover in the corners and along the edges of the enclosure.

Arboreal Salamander: All attacks were made very quickly. This predator initiated attacks on 50.0 percent of the prey presented. Of the total 20 attacks made, 12 (62.2%) were successful. These successful attacks involved seizing of the head or body. Unsuccessful attacks were made on the tail. The prey exhibited protean behavior in 91.7 percent of unsuccessful attacks and only 18.8 percent of successful attacks. Tail autotomy was only associated with unsuccessful attacks. The predator seized the tail and the prey, autotomized the tail and escaped. Following tail autotomy 75.0 percent of the tails were ingested. In one instance (25.0 percent) the tail was not ingested and the attack discontinued.

Clouded Salamander: No attacks were initiated by this species. This predator sought cover along the edges of the enclosure.

Black Salamander: No attacks were made by this species. It sought cover at the edges of the enclosure.

Rough-skinned newt: No attacks were made by this species. It sought cover at the edges of the enclosure.

Western Fence Lizard: This species attempted to escape from the enclosure and showed no interest in the prey.

Western Skink: This species also attempted to escape from the enclosure and showed no interest in the prey.

Northern Alligator Lizard: Although no attacks were initiated on the prey, each of the 3 predators approached and examined the prey during all tests.

Ringneck Snake: This species was the most efficient snake predator tested. This predator attacked 63.3 percent of the prey presented. Of the 19 attacks made 53.3 percent were successful. The speed of these attacks prevented determination of which body part was seized. The prey exhibited protean behavior in 83.3 percent of unsuccessful attacks and 8.3 percent of successful attacks. Tail autotomy occurred only during unsuccessful attacks. Following tail autotomy, 66.5 percent of the tails were ingested, 16.5 of the prey pursued, and 16.5 percent of the attacks discontinued.

Racer: This predator consistently approached the prey and exhibited considerable tongue flicking. The prey would slowly move away and seek cover at the edge of the enclosure. Two unsuccessful attacks were made. In both instances the prey quickly moved away and the attacks were discontinued.

Gopher Snake: No attacks were initiated by this predator. The behavioral response of this predator was identical to that of the racer. All prey were approached with a moderate amount of tongue flicking. The prey slowly moved away to the corner or side of the enclosure. The predator did not pursue the prey.

Common Garter Snake: This predator slowly approached the prey and then quickly attacked. Attacks were initiated on 33.3 percent of the prey. Of the total attacks made 72.2 percent were successful. The prey exhibited protean behavior only in unsuccessful attacks. Tail autotomy occurred during 11.1 percent of successful attacks and 100.0 percent of unsuccessful attacks. Following tail autotomy, 67.3 percent of the tails were ingested and one attack (33.3%) was discontinued.

Western Terrestrial Garter Snake: Attacks were made with moderate speed combined with a quick lunge when the predator was within 6 to 10 cm of the prey. Attacks were made on 40.0 percent of the prey presented. Of the total 12 attacks 54.4 percent were successful. All successful attacks resulted from seizing the head or body of the prey. The prey exhibited protean behavior in 8.3 percent of successful attacks and 100.0 percent of unsuccessful attacks. Tail autotomy occurred only during unsuccessful attacks in which the tail was seized. Following tail autotomy, 100.0 percent of the tails were ingested.

Western Aquatic Garter Snake: Attacks resembled those of the terrestrial garter snake. Attacks were initiated on 43.3 percent of the prey presented. Of the total 13 attacks 66.7 percent were successful. All successful attacks involved seizing of the head or body. The prey exhibited protean behavior in 6.7 percent of successful attacks and 100.0 percent of unsuccessful attacks. Tail autotomy only occurred during unsuccessful attacks. Following tail autotomy, 100.0 percent of the tails were ingested. No further attacks on the same prey were initiated.

Townsend Mole: Attacks were made very quickly. The prey was rapidly bitten on all parts of the body, probably resulting in a broken vertebral column. The prey appeared to die instantly and showed no movement. All attacks were successful and no protean displays were exhibited during any attacks. The speed of the attack did not allow for the prey to react. No prey tail autotomy was observed even though the tail was bitten many times.

Vagrant Shrew: Two of the predators violently attacked the first prey presented in a similar manner to the Townsend mole. The prey was bitten on all parts of the body and killed instantly. Following the single attack, both predators

retreated to a corner of the enclosure and began to wipe their mouths for 4 to 5 minutes. Although subsequently offered prey were investigated, neither of these animals made any further attacks. The third shrew investigated all prey but did not attack. Prior to and following testing with slender salamanders these predators readily accepted earthworms (Lumbricus terrestris).

Dusky-footed Woodrat: Both predators initiated one attack each on the first prey presented. Both attacks were unsuccessful and protean display occurred during both attacks. The 2 attacks inflicted wounds on the tail but no tail autotomy occurred. Following these attacks, one predator wiped its mouth for 3 to 4 minutes and the other retreated to a corner of the enclosure. Subsequent prey were investigated but not attacked.

Norway Rat: Two of the 3 predators reacted in a similar manner as the dusky-footed woodrat. Both wiped their mouths for several minutes following the first and only attack. One predator attacked the first 2 prey presented and then refused to attack all subsequent prey. All attacks were unsuccessful and the prey used serpentine movement to escape. No tails were autotomized by the prey. Subsequent prey were investigated but not attacked.

Black Rat: The predator made a single attack on the first prey and then discontinued the attack. This predator investigated subsequent prey but refused to attack subsequent prey. The attack was very short and the prey responded with serpentine movement.

Deer Mouse: No attacks were initiated by this predator. The prey and predator tended to seek cover in the corners or along the edges of the enclosure. The predator did not investigate the prey but rather tended to avoid the prey while attempting to find cover.

V. DISCUSSION

Limitations of Data

Surface activity data have several limitations due to the overall study design and sampling technique used. Data were collected from 11 characteristic sampling areas within each habitat type rather than intensively sampling a single area within each habitat. The average sampling area was about 10 m² and less than 4 minutes were allowed to check the cover and leaf litter at each sampling area. This approach resulted in a diffused sampling effort which yielded a lower recapture rate than would have probably been associated with a more intensive sample of a single area. Of the 668 animals marked in this study only 13.9 percent were recaptured more than once. Hendrickson (1954) sampled a single 148 m² area and reported a 51 percent recapture rate. Cunningham (1960) and Anderson (1960) also sampled 114 m² and 150 m² areas respectively and reported similar recapture rates. In each of these studies ground cover objects were added to each study area to facilitate the capture of slender salamanders. Of the 668 animals captured in this study 585 animals (87.6%) were found under cover objects. Therefore, the probability of capture and recapture would probably have been increased by placing more ground cover objects within a single area.

Seasonal and yearly variations in the climatic regime of a geographic area can influence the animal population within that area (Welty 1962:354, Porter 1972:254-256). Therefore, since this study only included a single spring and summer period, generalizations to annual cycles or average conditions cannot be made.

Surface activity was recorded from March through August 1971. Comparison with monthly mean rainfall for the same period for the years 1951-1960 (U.S. Weather Bureau 1960) indicated that monthly mean rainfall for March through May 1971 was 8.1 percent greater than normal. The June through August 1971 period was 1.0 percent greater than normal. Comparative ground temperature measurements for the area were not available. Hendrickson (1954) reported ground temperatures in his forested study area that were similar to those observed in the redwood forest habitat of this study (Figure 5). In general, the limited sampling period did not allow for statements to be made regarding the applicability of these data over an average annual cycle.

The data regarding protean behavior obtained from controlled laboratory situations should not be directly extrapolated to field conditions. The substrate, microclimatic conditions, light intensity and method of applying the stimuli differed in some respect from the natural environment. Also, behavior of recently captured animals in a confined space can be radically different from that observed in the field. Therefore, the consistency or irregularity of the protean displays may be in part due to experimental design. These same considerations apply to the predator-prey interaction experiments. Both predator and prey were in an unfamiliar space lacking cover. The greater speed of most of the predators placed them at selective advantage over the prey. Therefore, the success rate of attacks by predators may have been higher than would be expected in the field.

Although an attempt was made to simulate the light absorptive and reflective characteristics of a leaf litter substrate, the uniformity of the surface may have rendered the slender salamanders more visible and therefore more

vulnerable. The lack of cover may also have increased or decreased the intensity of the protean displays or affected some other component of this behavioral response. However, since predator-prey interactions are difficult to observe under field conditions, the use of captive animals in a controlled environment was the only feasible approach which would yield data regarding these interactions. The results indicate possible offensive and defensive strategies which were employed by these predators and slender salamanders in a confined space. Direct application of these data to predator-prey interactions in the field is not warranted.

Surface Activity and Temperature Preference

A positive correlation existed in this study between slender salamander surface activity and ground temperatures and rainfall. This same correlation has been reported by other workers (Hendrickson 1954, Anderson 1960, Cunningham 1960, Maiorana 1971). These studies have all indicated a peak in diurnal surface activity from January to February, the breeding period, followed by a gradual decrease until late May or early June, at which time the salamanders go underground and do not emerge until the fall rains. The cycle of surface activity observed in this study differs in several respects from that described for other studies: 1) the occurrence of nocturnal activity during wet spring months and 2) the continuance of a low level of diurnal and nocturnal surface activity throughout the drier summer months. Both these differences were probably due in part to the rainfall received in late June and the modifying influence of summer fog on both ground temperatures and relative humidity. Summer fog was not reported as a significant factor controlling summer surface activity in other investigations (Hendrickson 1954, Anderson 1960, Cunningham 1960,

Maiorana 1971). Due to the reduced number of samples conducted during July and August, no correlation between peak surface activity and summer fog could be detected. However, the increase in relative humidity and decrease in solar radiation associated with fog resulted in ground moisture and temperatures under which slender salamanders could forage on the surface and avoid desiccation, a significant source of mortality (Cunningham 1960, Maiorana 1977).

Comparison of the 3 habitat types indicated that diurnal surface activity in redwood forest was higher than in other habitats from June through August. This difference was probably due to the dense tree canopy. Ground temperatures for redwood forest during June through August were relatively stable, ranging from 10.0° to 14.5° C. Ground temperatures for the other two habitats were higher, ranging from 12.5° to 17.0° C for edge and 15.5° to 22.5° C for grassland/disturbed (Figure 5). Figures 5 and 6 and Table 4 show the relationship of ground temperature and tree canopy. Direct solar radiation heated 100 percent of the ground cover in open grassland areas, about 30 percent in edge and 15 percent in forest. The insulating effect of the redwood forest and edge canopy maintained lower ground temperatures and higher relative humidity (Waring and Major 1964), thereby providing a more suitable foraging environment for slender salamanders.

Nocturnal surface activity remained relatively constant from March through August (Figures 8 - 10). Hendrickson (1954:9) states that observations at night of animals in the field and those kept in terraria indicate low nocturnal mobility and activity. Similar findings were reported by Cunningham (1960) and Maiorana (1971, 1974). In redwood forest and edge habitats nocturnal activity began to approach the diurnal surface activity level from June through August.

In grassland/disturbed habitat the nocturnal activity level exceeded the diurnal activity level. The increase in nocturnal activity relative to diurnal activity appears to be related to the need to feed during periods of higher humidity and lower ground temperatures. Maiorana (1971,1974) reported a positive correlation between feeding activity and moist ground conditions. This relationship was very clear in the grassland/disturbed habitat. Increased ground temperatures and the resultant decrease in ground moisture almost eliminated diurnal surface activity in July and August. However, nocturnal feeding activity allowed those salamanders still active on the surface to feed at periods of lower temperature and increased relative humidity, with a concomittant reduced exposure of desiccation.

The reduction from March through August in diurnal surface activity in all habitats reflected both increased ground temperatures and decreased rainfall. Limited recapture data suggest that animals active from March through May were also active from June through August but at reduced levels. Although no age class differences were noted in animals active during these periods, Maiorana (1974) indicated that during the dry periods of winter immature animals were more active than adults.

Water loss from terrestrial salamanders is regulated to a major degree by their habitat selection and behavior, both of which appear to be influenced by rates of evaporation from the skin. The burrowing habit is extremely important to slender salamanders since soil moisture is a natural source of water for the animal and, while buried, evaporation from the skin is minimized (Porter 1972). During the dry periods of both winter and summer, slender salamanders go underground to escape desiccation (Hendrickson 1954). The increase in the humidity in the leaf litter and upper soil layer brought about by rainfall and/or fog probably serves

as the stimulus to bring the salamanders to the surface.

The temperature ranges under which slender salamanders occurred differed between field and laboratory conditions. Animals were found on the surface at temperatures ranging from 7° to 19° C. However, under laboratory conditions with relative humidity greater than 70 percent, slender salamanders from all habitats and during all seasons selected a narrower temperature range of 10° to 15.5° C. Animals collected in grassland habitat in August were recorded at temperatures from 5° to 6° C higher than the mean temperature selected by those same animals when exposed to a wider temperature gradient in the laboratory. In laboratory tests the lack of temperature preference differences noted between habitats and seasons suggests that this species has a temperature preference range which was unaffected by exposure to wider temperature ranges in the field. The fact that 62 percent of the animals found in the field were recorded at temperatures between 10° to 15.5° C also indicates a marked preference for a more moderate temperature range. Slender salamanders appear to have no "preferred" temperature but rather will generally accept the temperatures within their range of tolerance that happen to be available to them. In general, salamanders have the ability to alter their temperature tolerance range by acclimatization but otherwise there is no indication that they can control their temperature relations by any other means than behavior (Brattstrom 1963).

Determination of the monthly mean distance moved was influenced by: 1) most movements recorded were probably a function of the distances separating individual pieces of cover at each sampling area, 2) locating animals under cover objects was more successful than locating animals in leaf litter, and 3) the distribution of this cover influences the frequency distribution of the observed distances moved.

Due to the limited home range of this salamander, closely spaced cover objects increased the number of possible moves that would be easily detected. The cumulative effect of these factors was to produce a very conservative estimate of the distance moved.

The decrease from March through August in the monthly mean distance moved and the differences which occurred between habitats were probably due to decreased ground moisture and increased ground temperatures (Figure 11). The wetter ground conditions and lower ground temperatures of redwood forest and edge habitats allowed the animals in these habitats a wider range of surface activity with the reduced danger of desiccation. Maiorana (1977) has suggested desiccation as a significant mortality factor in slender salamanders. Even during March and April the grassland/disturbed habitat tended to dry out faster and so reduced the opportunity for surface moves between cover objects. In August ground temperatures above 17° C and the resultant decrease in ground moisture may account for the similarity in mean distance moved in edge and grassland/disturbed habitats.

The mean distance moved in redwood forest and edge habitat from March through May was about 47 percent lower than that reported by Hendrickson (1954) and Anderson (1960) in different habitats. The lower mean distance measurement I obtained was probably due to the sampling technique employed. By sampling a smaller area than they did, I reduced the potential for recording longer moves. Also, by not adding cover objects to each sampling area I did not increase the number of potential moves available to the salamanders in each sampling area, as they did. However, given the limited number of cover objects available to the salamanders in each sampling area, the decrease in monthly mean distance moved probably reflects an attempt to avoid exposure to desiccation.

The percentage of slender salamanders exhibiting protean behavior while being collected decreased at approximately the same rate in all habitats (Figure 12). Several factors were considered in determining the cause of the decrease: 1) the type of handling that was necessary to collect the animals, 2) the timing of the breeding season, and 3) possible decreased sensitivity of the protean display activating mechanism. A positive correlation was observed between rough handling and the number of protean displays elicited. Wet ground conditions from March through May made grasping the animals difficult, thereby increasing the likelihood of rough handling. A change in the collecting technique and drier ground conditions from June through August resulted in a decrease in rough handling. From late May onward salamanders were scooped up with the hand rather than grasped by some body part. When collected in this manner, animals did not attempt to escape and were much easier to handle. Figure 13 indicates a decrease from March through August in the monthly percentage of animals exhibiting protean displays when collected for the first time. Changes in collecting technique and handling occurred in late May. The rate of change between May and June does not appear to be different than other periods. Therefore, handling technique does not seem to explain this overall decline.

This decrease in protean displays may relate to the timing of the reproductive season. In the San Francisco Bay Area the breeding season for slender salamanders occurs from December to March (Anderson 1960). Based on limited observations of gravid females within the study area, the breeding season appears to occur during the same period. Therefore, in order to provide additional protection against predators during the critical breeding period, the protean display may

become more easily activated. As the breeding season ends, the activating mechanism may become less sensitive, thereby decreasing the number of displays recorded. However, the consistency of the protean displays elicited under controlled conditions during the same period (Figure 25) does not support this hypothesis. Recapture data indicated that an equal proportion of first time captures and recaptures occurred throughout the study period, thereby reducing the possibility that differences in the monthly capture rate of responsive animals lowered the number of protean displays. Therefore, it appears that a decrease in the sensitivity threshold of the protean display resulted in the decrease in number of protean displays recorded.

The extent of predation by snakes and salamanders as measured by the percent of animals active on the surface, with absent or regenerating tails, appears constant in all habitats from March through August (Figure 14). The increase in the percentage of animals with absent or regenerating tails reflects the fact that the tail remains lost for some time. Therefore, the monthly increase in the number of regenerating tails is cumulative. The significant increase from June to July in the percentage of animals with regenerating tails probably is related to the decrease in surface moisture and the differential decrease in surface activity of tailed and tailless animals. Tailless animals are forced to feed on the surface to replenish fat stores lost with the tail. The percentage of regenerating tails in various slender salamander populations studied has ranged from 30 to 80 percent, depending upon locality and season (Maiorana 1974). This percent range closely corresponds to the 24 to 74 percent range observed during this study. Vitt et al. (1977) has suggested that high frequency of tail breaks in natural populations of certain lizard species indicates the effectiveness of tail autotomy for predator escape.

Maiorana (1974) has documented that the tail of slender salamanders serves as fat storage important for reproduction in both males and females. Significant tail loss inhibits reproduction in mature individuals and delays maturity in immature individuals. If the tail was lost before the start of the dry season individuals regenerated new tails and failed to reproduce during the following breeding season. The mean rate of tail regeneration for slender salamanders is 1.5 mm per month (Hendrickson 1954). A slender salamander losing 20 mm of tail could regenerate all but 5 mm within the first year following tail loss.

Recapture data indicated that animals with regenerating tails were intermittently active from June to August. Those animals with complete tails were recorded only once during this same period. The lower percentage of animals with regenerating tails in redwood habitat was probably due to the lower ground temperatures and greater ground moisture which allowed a larger proportion of the total population to remain active on the surface. The drier conditions in July and August in edge and grassland/disturbed habitats significantly reduced feeding opportunities for slender salamanders (Figure 5). Although animals with complete tails were found in these habitats during this period, the increased proportion of animals with regenerating tails suggests that this segment of the population was forced to feed more frequently to maintain a minimum level of body fat stored throughout the summer.

Differences between habitats and seasons in the percentage of regenerating tails may in part be due to differential exposure to predation. Predators on slender salamanders were not uniformly distributed throughout all habitat types. Garter and ringneck snakes were primarily associated with edge and grassland/disturbed habitats. Based upon observation of predator-prey interaction, the Townsend mole

took entire individuals and therefore probably did not affect the percentage of animals with absent or regenerating tails. The Pacific giant and arboreal salamanders occurred in the redwood forest and edge habitats. Although the extent to which these predators prey on slender salamanders in the field is not accurately known, the distribution and relative abundance of these predators may exert a different predation pressure within each of the 3 habitats. Changes in the diurnal and nocturnal activity cycle of predator and prey may also be significant. The increase in nocturnal activity in grassland habitat may serve to decrease the slender salamander's exposure to the diurnal snake predators common in this habitat. Therefore, surface activity during dry periods of individuals with regenerating tails is seen as a compromise between the food acquisition required to regenerate the tail and avoidance of predators.

The watch-spring coil assumed by slender salamanders at rest was positively correlated with ground temperatures ranging from 7° to 14° C (Figures 15 and 16). Differences in the number of coiled animals between habitats and diurnal and nocturnal samples were related to the frequency of lower ground temperatures in these habitats. These animals were always found under cover with the head placed at the center of the coil. This posture resulted in a reduction in the total body surface area exposed. Although this posture would reduce water loss, the conditions at which 98.6 percent of the animals were found corresponded to periods of moderate ground temperatures and high rainfall and ground moisture (Figure 5). The increased retention of body heat was also unlikely to be of importance since these animals were always found under cover and were probably not exposed to air movement which would importantly increase evaporative water or heat loss.

However, this posture may serve to provide additional protection at lower ground temperatures from the hunting technique used by the ringneck snake, an important predator on slender salamanders (Stebbins 1954,1972). This snake is only slightly wider than the slender salamander and has been observed to feed under cover objects (Ruth 1977 pers. comm.) Based upon observations of captive slender salamanders body movement was decreased at temperatures below 9° C. About 73 percent of the coiled animals were recorded below this temperature. In animals with complete tails the coiled tail covered from 60 to 70 percent of the body. Of the animals recorded in this posture 63 percent had complete tails and 47 percent regenerating tails.

The relationship of the coiled posture with low ground temperatures is probably the result of the reduced mobility of slender salamanders at low ground temperatures and the concomitant increased vulnerability to attack from the ringneck snake while under cover. When encountering a slender salamander, a ringneck snake or other predator hunting under cover objects would be presented with an expendable tail. If an attack were made to the exposed tail, it could be autotomized and the salamander could seek cover within a burrow or the adjacent leaf litter. In an attack this posture probably provides protection to the head and body, increases the probability of a tail attack and allows the salamanders additional escape time. Also, under a cover object full protean behavior would be impossible, hence the need for a protective mechanism of similar efficacy.

Protean Behavior

Fleeing is the commonest behavioral response of prey animals to predatory attack. The effectiveness of fleeing can be improved by increasing speed, but many predators are faster than their prey. The prey's chances of escape then depends largely on protean behavior, particularly if no hiding place is immediately available. The adaptive nature of the single erratic protean response is most obvious when it occurs in direct response to a predator's attack. This response has been reported for several vertebrate species (Witherby et al. 1947, Tinbergen 1951, Kruuk 1964). However, the majority of the literature on this response deals with invertebrates (Marshall and Orr 1955, Humphries and Driver 1970, Edmunds 1974).

The single erratic response is triggered by a stimulus from the predator; it is a reaction to an emergency. In most populations studied the protean display response was not uniformly distributed throughout the population (Edmunds 1974). Only a portion of the population behaved in a random fashion when compared to the bulk of the population. Roeder (1959,1962) and Treat (1955), in describing random movements of noctuid moths that had detected the presence of hunting bats, provided an example of a protean display that was manifested by all members of a population. In slender salamanders the protean display exhibited under laboratory conditions appears to be uniformly distributed throughout populations existing in dissimilar habitat types and showed little seasonal variation.

The protean responses elicited by tactile stimulation of the tail consisted of both systematic and random components. The distance moved and duration of the display varied little between habitats and seasons (Figure 25). However, the direction of movement from the stimulus contact

point appears to represent the random components of the behavior (Figure 29). The relationship between distance moved and duration of the response was linear and systematic. These relationships indicate that the duration of movement may be physiologically determined. Changes in direction and distance of movement decrease the predictability of the response.

The decrease in the mean distance and time of movement for tactile stimulation of the body and head was a function of the manner in which the stimuli were administered. The tail of slender salamanders posterior to the hind limbs is cylindrical in cross-section. When the dissecting pin was placed into the tail the animals responded by rolling to one side, freeing themselves from the pin and then proceeded to exhibit protean behavior. When the pin was applied to the dorsal surface of the head or body, 34 and 14 percent respectively of the animals could not remove themselves from the pin and therefore were unable to respond. Comparison of responding animals indicated no significant difference in the time of movement but a significant decrease in the distance moved. This decrease in distance moved was also due to the responding animals' inability to free themselves from the pin. Therefore, due to these problems no statement can be made regarding differing sensitivities of the head, body and tail to tactile stimuli.

The lack of protean displays or other predator escape behavior exhibited in response to visual stimulation with potential predators suggests that visual recognition of predators is not an important component in the evolution of predator escape behavior in the slender salamanders. The reduction in visual acuity normally associated with a burrowing habit (Walls 1942, Porter 1972:82) supports this interpretation.

The protean display appears to be activated by both tactile and olfactory stimuli. The response of slender salamanders to the chemical extracts of potential predators indicates the evolution of an early warning system to detect the presence of efficient predators. Chemical extracts of the Pacific giant salamander, arboreal salamander, ringneck snake, common garter snake, western terrestrial garter snake and western aquatic garter snake elicited a significant number of protean displays in slender salamanders with regenerating tails (Figure 26). These 6 species also readily accepted and attacked slender salamanders throughout their captivity period (Tables 9 - 11). Slender salamanders tested were those which had presumably lost their tails to one of several species of predators which occurred within the study area. Since it was not possible to determine the predator which had taken the tail, all such animals were tested collectively. Since only one group of slender salamanders was tested with each chemical extract, the variability in the response may indicate the percentage of animals within the population which have lost their tails to various predators. However, the species' specific nature of the response was not investigated during this study. Amputation of the tail followed by testing with chemical extracts may be a means of testing the effects of tail loss on protean behavior. This aspect of protean behavior was not investigated. Olfactory recognition of potential predators by slender salamanders appears to be greatest in those predator species which are reported to prey upon slender salamanders in the field and laboratory. The nasolabial groove is suggested as the chemoreceptor organ which allows olfactory recognition of certain predators.

The nasolabial groove is a diagnostic characteristic in lungless salamanders. It extends from the latero-ventral

portion of the external nares ventrally to the upper lip. Associated with the nasolabial grooves are several nasolabial glands. Whipple (1906) thought that bucco-pharyngeal respiration was associated with the function of the nasolabial groove. Histological studies (Elkan 1958) have shown that the bucco-pharyngeal membrane of lungless salamanders lacks a capillary bed and is unsuitable for this purpose.

Salamanders have no external ears and their eyes are adapted for visual sensitivity rather than visual acuity (Walls 1942, Porter 1972:82-84). These characteristics suggest that olfaction may be of great survival value. The nasolabial groove and its associated structures constitute an apparatus which drains excess water away from the nares and thus prevents it from entering the nasal passages. This groove compensates for the absence of lungs and the breathing mechanisms which aid other salamanders in keeping the nasal passages free of water. The advantage of having free nasal passages is to allow full sensitivity to the nasal epithelium. Blockage of the nasal passage is a serious deterrent to olfaction (Brown and Martof 1966). Grant et al (1968) and Brown (1968) reported well developed chemoreception in both salamandrid and plethodontid salamanders. Brown (1968) indicated that fluids which pass over the nasolabial grooves are rapidly passed upward into the external nares. These fluids then pass over the chemoreceptors of the Jacobson's organ and down through the internal naris into the pharynx. This evidence strongly supports the idea that the nasolabial grooves in plethodontids directly facilitates chemoreception.

The variability of the protean response to olfactory stimulation indicated the following: 1) the response was not uniformly distributed throughout the population and 2) the olfactory response was learned. All test animals were taken from the study area and tested within 30 days from

the collection date. Prior to testing, exposure to all or none of the 6 predator species may have occurred. Comparison of the tail condition of animals responding to the olfactory response indicated that all protean displays were elicited from animals with absent or regenerating tails. Comparison of tail condition of animals responding to tactile stimulation showed no similar relationship. The recent loss of a tail would probably predispose the salamander to respond more quickly to the odor of a potential predator. Animals that recently lost tails were more sensitive to the presence of potential predators than were those with tails more fully regenerated and reacted without tactile stimulation. Stebbins (1954:398) indicates that the odorous substances secreted by the common king snake (Lampropeltus getulus) and other snake-eating colubrids are sensed by the western rattlesnake (Crotalus viridis), resulting in the characteristic retreat of the rattlesnake with the head close to the ground. This response is seen only in rattlesnakes from areas within the king snake range, suggesting a learned response.

Comparison of the protean displays elicited by tactile and combined olfactory/tactile stimuli showed a significant increase ($22.5 \pm 9.2\%$) in the mean distance moved but no significant change in the mean time of movement (Figure 27). These data suggest that the combined olfactory/tactile stimulus activated a response of greater physiologic intensity. These observations support the hypothesis that tactile and combined tactile/olfactory stimuli can result in protean displays in which the effects may be additive or synergistic in releasing the display and in determining the violence of the display. Tail loss may lower the threshold for overt reaction to these stimuli and hence to start the protean display. The distance moved is a measure of the physiologic intensity of the display. Comparison of

linear regressions and correlation coefficients for tactile and combined olfactory/tactile stimuli indicates a higher correlation coefficient for the olfactory/tactile response. Therefore, the increased correlation in the linear relationship between duration of movement and distance moved suggests that the distance moved was a function of increased intensity of the movement due to olfactory recognition of predators. The lack of difference between the response of animals with and without recent tail loss suggests that olfactory recognition of certain predator species is present throughout the entire population, regardless of previous predator contact. The mechanism responsible for this generalized recognition of predators may possibly be genetic.

Therefore, olfactory recognition of certain predators appears to be present within the entire population but can be increased by recent tail loss. Animals which have recently lost tails cannot use tail autotomy when encountered by predators. Since they are forced to feed on the surface to replace fat stores lost with the tail, they are exposed to continued predation. The lack of a tail decreases the number of defense strategies which can be employed by these animals and may result in increased sensitivity in olfactory recognition of potential predators.

Photographic Analysis

Photographic analysis of the protean displays elicited by an electric shock revealed 3 distinct types of behavior: 1) body avoidance, 2) serpentine movement and 3) protean display. Since an electric shock constitutes a stimulus with which these animals were unfamiliar, the interpretation of these responses must be viewed cautiously.

Body avoidance was dissimilar from the reaction observed in head and body stimulation. The body part was

quickly withdrawn from the probe in a manner similar to withdrawing one's hand from a hot object. No attempt was made by the slender salamanders to escape from the stimulus. The response appears to be a pain avoidance reaction. Serpentine movement was a direct attempt to escape from the stimulus. The movement started with tail wagging, followed by intense lateral undulations. Limbs were used intermittently during serpentine movement primarily during the less intense final movements. No sequence in the use of front or hind limbs was noted. The significance of the tail wagging at the start of serpentine movement is questionable. The duration of this tail wagging (0.09 to 0.18 s) may draw the predator's attention to the expendable tail, thereby increasing the slender salamander's chances of escape. Observations of predator-prey interactions indicated that snake predators used quick attack strategies but amphibian predators were considerably slower. The duration of the tail wagging response would appear to be significant only for predators with quick reflex reaction time. Physiological studies of snake and amphibian predator reaction time and visual acuity are needed to support this hypothesis. The rhythmic undulations of serpentine movement generally also appeared to draw attention to the tail and increased the salamanders' escape speed.

The reduction in size of the limbs in slender salamanders is in part due to its burrowing habit (Maiorana 1974). Normal locomotion in slender salamanders with the use of such small limbs is very labored. Gans (1962) has discussed the evolution, mechanics and effectiveness of limbless locomotion. He notes that lateral undulations seem to be the first step in a species evolving toward limblessness. The use of earthworm burrows by slender salamanders for estivation and cover throughout the year (Stebbins 1954, Maiorana 1974) would support the need to develop limbless

locomotion. As a predator escape mechanism, serpentine movement clearly increased the speed of the escape and appears to provide the slender salamander with additional time to seek cover in the leaf litter or under cover objects.

Protean displays were so variable in their components and sequences as to defy systematic description. The increase in the number of protean displays elicited by electric stimuli applied to the tail, body and head suggests an increasing sensitivity from the tail to the head. Nearer the head the neurological effects of electric stimulation are probably greater and account for the increased number of displays. The initial sequences involved tail wagging followed by a series of violent lateral undulations which threw the animal into the air. The lack of a discernible relationship between head and tail position with respect to the stimulus contact points suggests that these movements are random. The use of both serpentine movement and motionless ending for the protean displays appears to increase the variability of the response. A predator would probably have difficulty in following such a short (1.02 s) and rapid response. Once the protean display was completed, the slender salamander could remain motionless, relying on its cryptic coloration or quickly escape into a burrow or the leaf litter. Both behaviors were observed while collecting slender salamanders in the field.

The protean display appears to contain a wide range of components which are used singly or in combination to increase the variability of the response. Animals that employ all of the behavioral components of the display may be at selective advantage over those animals using a smaller number of components. The lack of predictability of the protean display probably insures against learned counter responses by predators.

Prey Palatability and Toxicity

The secretion of toxic substances by the venom and mucous glands of salamanders has been documented by many workers (Webster 1960, Brodie 1968a, 1968b, Brodie and Gidson 1969). In slender salamanders these glands either do not occur in sufficient numbers or contain a low toxicity venom which is not lethal when ingested. No mortality occurred in selected vertebrates with force feeding of a 30-mm section of slender salamander tail or body. Slender salamanders do not appear to employ lethal biochemical defenses to discourage attacks by predators.

The potential predators tested showed differential palatability for slender salamanders. Species known to prey upon slender salamanders in the field or laboratory (Table 9) required little or no effort during feeding. These species included the Pacific giant salamander, arboreal salamander, ringneck snake, common garter snake, terrestrial garter snake, aquatic garter snake and Townsend mole. Of this group only the Townsend mole has not been previously reported to feed on slender salamanders. Comparison of the results of force feeding (Table 7) and predator-prey interactions (Table 9) indicated that the gopher snake and racer readily ingested slender salamanders but did not initiate any attacks on them in the laboratory. The refusal of these predators to initiate attacks may indicate that the slender salamander is not normally preyed upon by them.

Species not known to prey upon slender salamanders rejected the prey by refusing to swallow and immediate or delayed regurgitation. This group included rodents, shrews, lizards and insectivorous salamanders. Comparison of Tables 7 and 9 indicates that those potential predators which showed low palatability for slender salamanders did

not initiate attacks on them in the laboratory. This relationship suggests that slender salamanders are not preferred prey for these species. The regurgitation of fed salamanders suggests that a secretion in the skin of slender salamanders may be responsible for this reaction. Reduced prey palatability in this study appears to effectively discourage attacks by certain potential predators. Edmunds (1974) cited different palatability of prey for various vertebrate predators. The extent to which regurgitation of prey occurs in the field and the mechanism which initiates the response was not investigated.

Tail Autotomy

A variety of vertebrates and invertebrates have the ability to constrict and break off a part of the body when attacked (Edmunds 1974). If the predator is left with the autotomized body part while the prey escapes, the defense has succeeded in protecting the prey and also feeding the predator. In the slender salamander populations studied to date, no instance of tail autotomy due to rough handling has been reported (Maiorana 1974). However, the percentage of animals with absent or regenerating tails in various populations has ranged from 30 to 80 percent. The fact that rough handling does not result in tail autotomy would suggest that the mechanism is far more specific than in species of skinks and geckos which readily lose their tails with rough handling (Stebbins 1954, Edmunds 1974, Vitt et al. 1977).

The tail of plethodontid salamanders functions in locomotion, food storage, respiration, defense and courtship. Tail autotomy as a defense against predators is widespread throughout the family. Its importance as a defense mechanism is attested by the fact that a number of anatomical

specializations are associated with tail breakage (Wake and Dresner 1967). A wound healing specialization involves a breakage pattern of the tail in which the skin breaks at the posterior end of the segment and the muscle at the anterior end. A cylinder of skin is left with the intact part of the tail; the skin folds down, facilitating blood clotting, protection of the wound and subsequent healing and regeneration. Slender salamanders have developed wound healing specializations which allow the tail to be autotomized at any point (Wake and Dresner 1967).

The responses of slender salamanders to mechanical severing of the tail were similar to those elicited by tactile and electrical stimuli (Tables 6 and 8 and Figures 19 - 25). Lack of movement after tail autotomy was only observed in this experiment.

The protean response following tail autotomy may be an attempt to further confuse the predator by presenting 2 moving objects. The tendency was for the predator to attack the closest moving object, the tail. This was observed during actual attacks by predators on slender salamanders (Table 12). Since the tail continues to move even if held in the predator's mouth, this movement may also provide a stimulus which simulates the movement of a struggling captured slender salamander. The movement of a seized tail may suppress the predator's motivation to initiate an attack on the escaping salamander. The reaction of predators to autotomized tails (Table 12) supports this hypothesis since 80 percent of the predators ingested the autotomized tails and did not continue to pursue the prey.

The range of responses of slender salamanders following tail autotomy appears to provide a series of behavioral responses which can be used in a wide variety of predator-prey interactions.

Predator-Prey Interactions

A number of offensive and defensive strategies were used during predator-prey interactions. A comparison of Table 9 and Figure 26 indicates that the chemical extracts of those species which elicited protean displays were the same species which initiated 3 or more attacks on slender salamanders. The correlation between olfactory recognition by the prey and the increased number of attacks initiated by the predator supports the hypothesis that slender salamanders have evolved an early warning system to detect the presence of those predators that prey most heavily on them. Since a chemical extract of the Townsend mole was not prepared and tested, no comparative data were available to determine whether the same relationship applies to this species.

The greater success in capturing the entire salamander, of predators that made head and body attacks as opposed to tail attacks, suggests that behavioral responses which draw attention to the tail of slender salamanders may minimize the probability of a fatal head or body attack. Since protean displays were used in 10.0 percent of successful attacks and 79.2 percent of unsuccessful attacks, it appears that the use of protean displays increased the probability of unsuccessful attacks. Tail autotomy resulted from the tail being seized by the predator, followed by a protean display which provided the force necessary to autotomize the tail. Tail autotomy appears to be used as a last line of defense which allows a non-essential part of the body to be lost during emergency. The importance of the tail in the reproductive physiology of slender salamanders may account for the limited number of tails autotomized during predator-prey interactions.

A correlation exists between the geographic ranges of predators which initiated attacks and slender salamanders. Those predator species which initiated the greatest number of attacks occur throughout major portions of the slender salamander's range. The predators initiating attacks included: the Pacific giant salamander, arboreal salamander, garter snake, ringneck snake and Townsend mole. This relationship was not as evident for predator species which did not initiate attacks.

The ranges of the Pacific giant salamander and the slender salamander overlap in coniferous forest along the coast from Monterey Bay, California to Gold Beach, Oregon. The arboreal salamander's range is identical to that of the slender salamander. Based upon personal observations within the study area, surface activity periods of these 2 predators were comparable to those of slender salamanders. The response of slender salamanders, which occur outside of the range of the Pacific giant salamander, to chemical extracts of this predator would provide additional insight into the evolution of this predator-prey relationship.

Garter snakes were effective predators on slender salamanders and occur throughout its entire range. However, since these snakes are generally active during the day from about March to October, the January to February peak in slender salamander surface activity is missed. The ringneck snake was the most effective snake predator tested. The range of the ringneck snake closely overlaps that for the genus Batrachoseps (Stebbins 1954, 1972). The response to the ringneck snake of the northern species B. wrighti and the southern species B. major should be studied.

Of those animals tested, the Townsend mole was the most effective predator on slender salamanders. Anderson (1963) reported a similar reaction of the California mole to slender

salamanders. The ranges of the Townsend mole and slender salamander overlap along the coast from Point Arena, California to Port Orford, Oregon. The California mole does not occur widely in this area but is common throughout the remainder of the slender salamander's range (Stebbins 1954, Engles 1965). Although these moles normally occur in well drained meadows and valleys, they are also found in clearings within deciduous and coniferous forest (Burt and Grossenheider 1964). Since moles are largely fossorial (Engles 1965), and slender salamanders may occupy earthworm burrows (Stebbins 1954:63) when not active on the surface, moles may frequently encounter slender salamanders underground. Slender salamanders would be severely limited in the escape behavior that could be used when encountered by moles underground. The extent to which moles feed on slender salamanders in the field has not been documented.

VI. CONCLUSIONS

In the habitat types investigated: 1) second growth redwood forest, 2) grassland, and 3) the forest/grassland edge, surface activity of slender salamanders was positively correlated with rainfall and with the lower ground temperatures observed. Cool, moist ground conditions provided a suitable environment for surface activity. Summer fog did not seem to be correlated with dramatic increases in surface activity, but it probably served to maintain lower ground temperatures and increased ground moisture which permitted a low level of surface activity to continue throughout the summer. Greater surface activity by slender salamanders occurred in the cooler, moister forested habitat throughout the study period. Temperature preference studies conducted in the laboratory indicated that at a relative humidity greater than 70 percent, slender salamanders selected a narrower temperature range (10° to 15.5° C) than that recorded in the field (7° to 19° C). Slender salamanders appear to have 5.5° C preferred temperature range but will be active on the ground surface at most temperatures within their known tolerance range (7° to 21° C).

From March through August diurnal surface activity declined at differing rates in each habitat but remained highest in redwood forest, followed by edge and grassland habitats. Nocturnal surface activity remained relatively constant in all habitats from March through August. Limited data suggest that this species becomes nocturnal during the drier summer months.

In all habitats the monthly percentage of animals with absent or regenerating tails increased from March through August. This change was due to the necessity of animals with regenerating or absent tails to continue feeding on the

surface to replenish fat stores required to regenerate the tail. Animals with complete tails appear not to be forced to feed on the surface during dry periods and thereby account for a smaller percentage of such animals found during these periods.

Protean displays exhibited by slender salamanders were tested using tactile, visual and olfactory stimuli. Response to tactile stimuli indicated that the direction of the movement from the point at which the salamander was located when the stimulus was applied appeared to be random. The time of movement of the protean display varied slightly, but the distance moved varied considerably. Time and distance of movement generally followed a linear relationship. Visual stimulation with potential predator species in a sealed plastic box resulted in no significant behavioral responses. The response of slender salamanders to chemical extracts of potential predator species indicated olfactory recognition by slender salamanders of predators known to prey upon them in the field and laboratory. Overt responses of slender salamanders to chemical extracts of potential predators was greatest in animals with recent tail loss. Combined olfactory/tactile stimulation of animals, both with and without regenerating tails, resulted in an increase in the mean distance moved from the stimulus contact point when compared with olfactory stimulation of salamanders with regenerating tails. The increase in the physiological intensity of the display probably accounted for the increased distance moved. Therefore, olfactory recognition of potential predators appears to exist throughout the entire population, but the threshold of the response can be lowered by the recentness of tail loss.

Increased olfactory recognition of predators following tail loss may indicate a lowered stimulus threshold for the protean display. The lower level of olfactory recognition

present throughout the entire population may indicate a genetically controlled response. These data suggest the evolution of an early warning system which gives olfactory recognition of certain predator species both prior to, during and after an attack.

High speed photographic analysis of reactions to electrical stimuli were classified into these components: 1) body avoidance, 2) serpentine movement and 3) protean display. Serpentine movement and protean display consisted of initial tail wagging movements which may draw the attention of predators to the tail. Following tail wagging, protean displays also utilized random head and tail movements which would appear to have the function of confusing predators.

Force feeding of slender salamanders to 22 potential predators indicated variable palatability but no serious toxic effects. Those predator species to which slender salamanders responded in the olfactory stimuli tests also readily fed on slender salamanders in the laboratory. Prey palatability was highest for carnivorous salamanders, snakes and moles, and lowest among rodents, shrews, lizards and insectivorous salamanders.

Twenty-two potential vertebrate predators were used to test the type of predator escape behavior exhibited by slender salamanders during an actual attack by a predator. Successful attacks in which the entire salamander was ingested were made to the head and body. Unsuccessful attacks in which the salamander escaped with or without its tail were made on the tail. Tail autotomy occurred only when the predator seized the tail. The protean display which followed the predator's seizing of the tail provided the force to autotomize the tail. The protean display was effective in reducing the number of successful kills. The display appears to delay components of the predatory

response by providing conflicting neurological stimuli to the predator. The protean display probably insures against learned counter measures by incorporating variability as a basic behavioral component. Prey which employ a wide variety of behavioral patterns unfamiliar to the predator will be at a selective advantage.

VII. LITERATURE CITED

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