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Orientation and flight behavior of a Neotenic Salamander (Ambystoma gracile) in Oregon

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ABSTRACT: Neotenic *Ambystoma gracile* in lakes containing predatory trout was less abundant and less active than in lakes not containing fish. I quantified flight behavior in two populations, one exposed to fish and one not exposed to fish, focusing on direction faced and direction of flight with respect to lake morphology, and burrowing behavior at the end of the flight movement. I investigated relationships among behavior, water depth and substrate. Independence among behavioral alternatives was also evaluated. Both populations displayed significantly nonrandom behavior; the two populations differed in most behavioral components. Both populations faced toward deep water more often than could be expected by chance. In the absence of fish, 96% of the salamanders responded to simulated attack by moving into deeper water or by burrowing into the substrate. In the presence of fish, flight into shallower water was more frequent than expected by chance; alternatives of flight direction were dependent upon water depth in large (older) salamanders. Though burrowing for refuge was less frequent in the population exposed to fish, frequency of burrowing increased with water depth. Different frequencies of flight behaviors in the two populations are responses to differential predation pressure.

INTRODUCTION

When attacked by a predator a prey may take refuge, flee, or retaliate with some behavior that will otherwise thwart the attack. Variations on the third alternative have fascinated many observers (reviewed by Edmunds, 1974), but the second option is most common in motile animals (Humphries and Driver, 1970). There is little quantitative information on fleeing behavior, however, even though analyses of predator efficiency indicate that flight is often a successful response to predator attack (Curio, 1976). The purpose of the present study was to quantify orientation and flight behavior in neotenic *Ambystoma gracile* in lakes of the Cascade Mountains of Oregon. Flight here is restricted to movement away from a point of attack.

Ambystoma gracile is normally one of the top carnivores in lakes in the Cascades, although semiaquatic predators such as snakes, birds or water shrews may occasionally prey upon it (pers. observ.). In recent years most Cascades lakes have been stocked with trout *(Salmo, Salvelinus)* which prey upon the neotenes (Effort and Mathias, 1969; Sprules, 1974; pers. observ.). I compared two populations of *A. gracile;* one was subject to fish predation and one was not.

Observations tested the general hypothesis that orientation and flight direction are random in both populations. Acceptance of the hypothesis would invoke two possible explanations: either flight behavior is not a functional defense against predation in *Ambystoma gracile,* or the most important component of such behavior is its unpredictable or protean nature (Chance and Russell, 1959). Rejection of the hypothesis would indicate that certain behaviors provide better protection from predation than others. Differences and similarities between populations would measure the relative plasticity of flight behavior.

Study areas. — In a survey of 32 lakes containing trout, Fay Lake (Linn Co., Oregon, R7E, T12S; elevation 1166 m; 3.5 ha, maximum depth 4.5 m) exhibited the greatest density of *Ambystoma gracile.* Extensive patches of *Isoetes* and a few other rooted plants grew in the shallows; otherwise the soft mud bottom was bare. The lake is stocked biennially with fingerling trout though some stockings fail (*e.g.,* the 1973 stocking was air dropped into 27 C water; the bottom was immediately littered with dead fish, and I never saw a live fingerling that summer). Dark Lake (Jefferson Co., Oregon, R8E, T13S; elevation 1134 m; 4.5 ha, maximum depth 13.5 m) had a soft silty mud bottom virtually devoid of vegetation, and contained no fish. All observations on flight behavior were made in these two lakes.

I also worked at Scout Lake (3.5 ha, maximum depth 7 m; no fish), Scott Lake (5 ha, maximum depth 8 m; trout present) and Lost Lake (25 ha, maximum depth 5 m; trout present). All study lakes lie within 9 km of the crest of the Cascade Mountains; greatest distance between any two lakes is 24 km.

METHODS

I used skin-diving and scuba equipment to observe salamanders. In lakes containing fish, *Ambystoma gracile* is almost exclusively nocturnal (Sprules, 1974), so for comparative purposes all behavioral observations were made at night, usually with a 6 V diving lantern for illumination. Some observations in shallow water were made on bright moonlit nights without a lantern, or with a Javelin Model 221 night-viewing device in a waterproof case. Comparison of observations with and without the lantern indicated that there was no difference in salamander behavior due to artificial illumination.

In Fay Lake I worked on two 30 x 50 m quadrats located in areas of greatest salamander density. In Dark and Scout lakes observations were made on two 3 x 30 m transects established on the 2 m and 6 m isobaths. Observations in the other two lakes were made on 3-m-wide transects from shore to the deepest parts. For density estimation I established 3 x 30 m transects at 0.7 m in one of the Fay Lake quadrats, in the deepest part of Fay Lake and at 10.5 m depth in Dark Lake.

Upon finding a salamander I recorded its relative size (small, medium or large), the type of substrate upon which it rested and the aspect of the head (toward shore, toward deep water, lateral to shore). I then touched the animal on the dorsal midline in the pectoral region with the end of a 3 x 300 mm rod, and recorded the direction of escape, whether or not the animal burrowed into the substrate at the end of the movement, and the type of substrate. A preliminary study indicated that the elicited escape was a true startle-response unbiased by my presence, as the salamanders were as likely to move toward (under) me as away from me. Orientation, as indicated by head aspect, was included in the study since position of a prey just prior to attack may define its possibilities of escape, and in itself may constitute an antipredator defense.

In Fay Lake I marked the positions occupied by the startled salamanders with numbered flags, returning the next day to measure water depths at those points. No such measurements were taken in Dark Lake, but the depth occupied by each salamander observed was known to within ± 0.5 m due to use of the established transects.

Samples of animals were taken from Fay, Dark and Scout lakes for morphometric analysis. These specimens were anesthetized, weighed, measured and preserved within 30 min of the end of the dive during which they were captured.

The study lakes freeze in winter; observations began after ice-out. Observations reported here were made in the periods 22 June-23 September 1975; 25 May-9 July 1977; or 21 July-15 August 1978.

On my first dives of the year I found many *Ambystoma gracile* egg masses. At Fay Lake I spent the 1st 2-4 days each year counting and marking all egg masses with colored flagging. Reproductive behavior after observations began would then be manifest by appearance of unflagged egg masses.

I originally analyzed all behaviors by size class. While there were apparent inconsistencies between some groups with respect to randomness, contingency table analysis indicated that, with a single exception, the behavioral frequencies were independent of size class within a lake. I therefore combined homogeneous frequency data for all size classes within a lake. Associations with depth were analyzed separately by class.

The principal statistical technique employed was chi-square goodness of fit. Expected behavioral frequencies were generated from contingency tables when comparing the two populations or testing for independence of behaviors. Orientation and escape direction were tested against a randomly expected proportion of 1 toward shore: 1 toward deep water: 2 lateral to shore, since there were 2 quadrants of lateral behavior to 1 quadrant each for the other alternatives. Expected frequencies of behavior for each substrate type were generated from percent occurrences of the substrate type on line transects (McIntyre, 1953).

RESULTS

In the two lakes lacking fish I found *Ambystoma gracile* at all times of the day and night except in shallow water, which they entered only at night (Table 1). In the three lakes with fish *A. gracile* was seen only at night in water no more than 1.3 m deep. On the 10.5 m transect in Dark Lake I saw up to 10 times as many salamanders per unit area as were seen in Fay Lake. Densities in Scott and Lost lakes were so low that sometimes 20 min of underwater search were required to find a single animal.

On my first dives of the year in fish lakes I found egg masses attached to objects in the deepest parts, although no *Ambystoma gracile* was ever seen there in over 100 hr of nocturnal observation. Apparently in early spring the salamanders will enter deep water to deposit eggs when trout are present. I never saw them do this; egg deposition was completed by the time I gained access to the lakes, as no unflagged egg masses were ever found.

While the populations not exposed to fish had much greater densities, they were composed of much less robust individuals (Fig. 1). For any given snout-vent length the animals from Fay Lake were significantly heavier than those from the fishless lake (analysis of covariance of log transforms, location effect on slope F = 181.1; 1, 126 df; $p < 0.001$). There was no difference between Scout and Dark lake animals in this respect, nor were there differences between sexes within a lake. Fay Lake salamanders do not appear to be experiencing resource depression when compared to animals from fishless lakes, where competition for food is apparent.

I observed 626 aspects and 624 flight behavior sequences in Fay Lake, and 560 of each in Dark Lake (Table 2). Both populations deviated significantly from randomness in their orientation, with a tendency to face toward deep water. There was no significant difference between the two populations in this behavior.

Flight behavior frequencies of small and medium animals in Fay Lake deviated

TABLE 1.—Means ± standard errors of numbers of *Ambystoma gracile* seen on 3 x 30 m transects

Lake	Depth	Day	Night
Fay (fish)	0.7 m	0	4.8 ± 1.7 (A)
	> 1.5 m (B)	0	0
Dark (no fish)	2 m	1 seen in 10 transects	33.0 ± 5.6
	6 m	1 seen in 10 transects	42.2 ± 12.2
	10.5 m	35.8 ± 5.6	50.3 ± 5.5
Scout (no fish)	2 m	0	28.7 ± 2.4
	6 m	6.3 ± 3.4	27.0 ± 6.1

(A) Does not include observations for August and September, 1975, when densities were lower following a successful fish stocking

(B) Transects through deep water were between 80 and 270 m long, including the swim to the established transect significantly from those of large salamanders, so the two groups are presented separately (Table 2b). Escape direction was significantly nonrandom; there was also a significant difference between behavioral frequencies of the two populations (smaller animals, $X^2 = 19.0$; large animals $X^2 = 14.1$; $p < 0.001$, 2 df for both). Both groups of Fay Lake salamanders tended to flee toward shore, with some overrepresentation of fleeing toward deep water by large salamanders. Dark Lake salamanders tended to flee toward deep water. Due to the continuous slope of the bottom in both lakes, flight toward deep water was movement into deeper water; flight toward shore was movement into shallower water.

The dichotomy of flight behavior preferences in large Fay Lake animals was associated with depth (Fig. 2). Average depth occupied by large animals fleeing toward deep water was 79 cm (SE = 4.6); those fleeing toward shore averaged 67 cm (SE = 3.6). The significant difference between averages ($t = 2.05$, $p < 0.05$, 74 df) reflects the fact that animals in the shallows tended to flee toward shore, while animals in deeper water moved into even deeper water. The average depths occupied by small and medium salamanders fleeing toward deep water were also greater than those occupied by their shoreward-moving fellows, but the differences in these groups were not significant. In Dark Lake no flight behavior frequencies observed on the 2-m transect differed significantly from those recorded on the 6-m transect.

There was a strong relationship between head aspect and direction of flight in both populations. This relationship can best be illustrated as propensity for straight ahead flight as a function of head orientation (Table 2c). Fay Lake salamanders had a strong tendency to flee straight ahead if facing toward shore, and to turn to flee if oriented laterally. The Dark Lake salamanders tended to flee straight ahead if facing deep water, and to turn if oriented otherwise. This latter tendency was not due to the

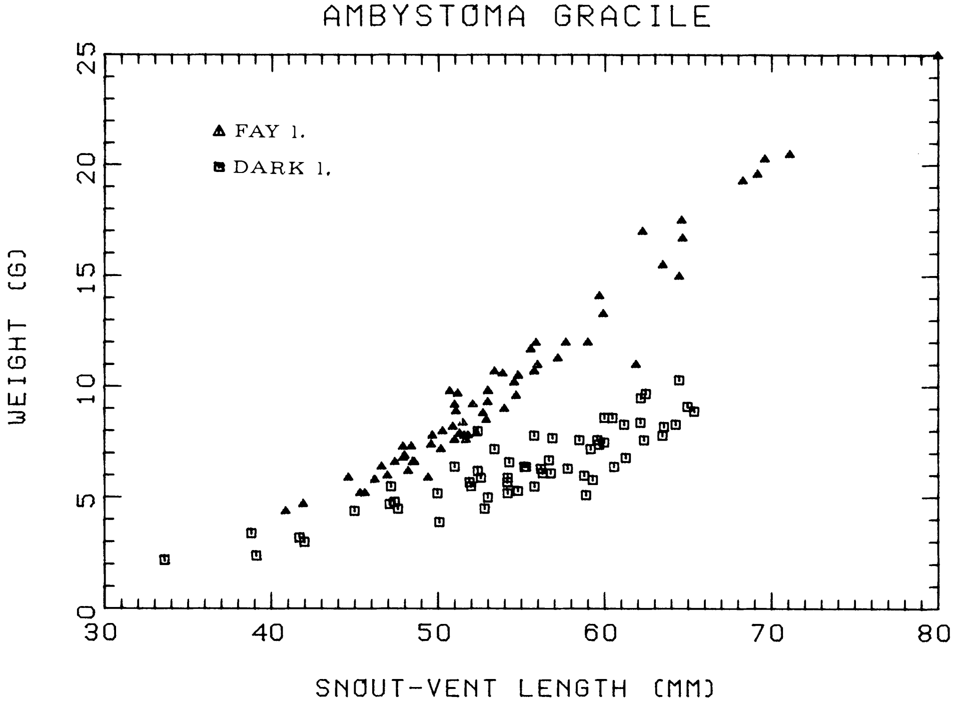

Fig. 1.—Nutritional status of Fay Lake and Dark Lake salamanders

preference for fleeing toward deep water, since it was also based on a number of animals that turned to flee in a direction other than toward deep water. The differences in flight behavior tendencies of the two populations were highly significant.

Table 2 reveals a consistent attribute of orientation and flight behavior: underrepresentation of the lateral or parallel to shoreline alternative. In both populations lateral head aspect, lateral flight and straightforward flight when oriented laterally all occur much less frequently than would be expected if the salamanders were behaving randomly.

The last component of flight behavior was position at the end of the movement. The majority of salamanders in both lakes burrowed into the substrate, but there was a significant difference between populations in the frequency of this behavior also: 206 of 624 Fay Lake animals (33%) remained on top of the substrate while only 58 Dark Lake salamanders out of 560 did so. This behavior was independent of flight direction in Fay Lake, but not in Dark Lake ($X^2 = 16.82$, $p < 0.001$, 1 df), where animals fleeing laterally or toward shore were over 2.5 times more likely to burrow than were those fleeing toward deep water. Most burrowing animals penetrated the substrate so deeply that efforts to touch them again by groping were futile.

The tendency of the Fay Lake salamanders to burrow was associated with depth (Fig. 3). The probability that a salamander would seek refuge in the mud increased as depth increased.

There was no detectable association of any behavioral alternative with type of substrate.

TABLE 2.—Orientation and escape frequencies

	Fay Lake			Dark Lake		
	Observed	Expected	χ^2	Observed	Expected	χ^2
a) Orientation:						
Toward shore	160	157	.1	143	140	.1
Lateral to shore	273	313	5.1	250	280	3.2
Toward deep water	193	157	8.5	167	140	5.2
		Total:	13.7**			8.5*
b) Escape:						
Small & medium animals				All animals		
Toward shore	155	130	4.9	120	140	2.9
Lateral to shore	222	260	5.4	222	280	12.0
Toward deep water	142	130	1.2	218	140	43.5
		Total:	11.5**			58.3***
Large animals						
Toward shore	40	26	7.2			
Lateral to shore	29	53	10.5			
Toward deep water	36	26	3.6			
		Total:	21.3***			
c) Straight forward escape:						
Toward shore	104	87	3.5	63	74	1.6
Lateral to shore	133	150	1.8	115	129	1.5
Toward deep water	105	106	0	111	86	7.1
		Total:	11.8**(A)			21.2***(A)

* $p < .05$
** $p < .01$
*** $p < .001$
(A) Data reported are one half of a contingency table

DISCUSSION

The much lower densities and temporally restricted activity of the three populations exposed to fish are striking when compared to those in the lakes without fish. In the presence of fish, *Ambystoma gracile* was seen only at night, in the extreme shallows, in relatively low numbers. In the absence of fish, *A. gracile* was found in the depths day and night, at much higher densities. These observations are consistent with others. Efford and Mathias (1969), Neish (1971) and Efford and Tsumura (1973) noted almost exclusively nocturnal behavior, as well as trout predation, of *A. gracile* in Marion Lake, B.C. Sprules (1974) found lower relative densities and restriction to nocturnal activity in *A. gracile* exposed to fish in other British Columbian lakes. The Marion Lake workers also found concentration of *A. gracile* in areas <2 m deep, though on occasion they trapped this species at depths exceeding 4 m.

When one species is restricted in habitat usage and activity and occurs at lower density in the presence of another species, one must consider the possibility of interspecific competition. Indeed, Efford and Tsumura (1973) and Eagleson (1976) have speculated about potential (exploitation) competition for food between *Ambystoma gracile* and trout. That Fay Lake salamanders were much more robust than animals from fishless lakes indicates that exploitation competition for food is not the major interaction between *A. gracile* and trout. Lower densities and restricted activity in the presence of trout are consequences of predation.

The depth associations and escape movements of Fay and Dark lake salamanders are distinctly different, suggesting that they are responses to different types of predation. During the day *Ambystoma gracile* was found only in deep water in Dark or Scout lakes. When startled at night, most Dark Lake salamanders fled into deeper water. Deep water should provide refuge from terrestrial predators with limited diving ability and time for underwater search. Avoidance of the shallows during the day may be avoidance of diurnal predators. Alternatively, there may be little food in the shallows during the day, and activity there at night may be associated with the well-known ver-

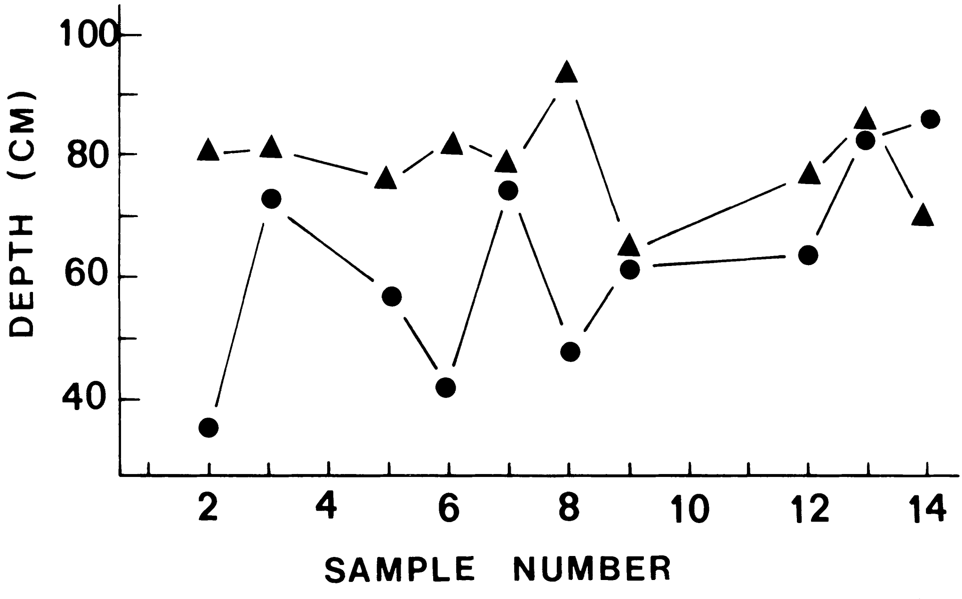

Fig. 2.—Average depths occupied by large Fay Lake salamanders escaping toward shore (circles) and toward deep water (triangles). Each point represents a minimum of three observations

tical migration of zooplankton. *Ambystoma gracile* does feed on zooplankton, particularly cladocera (Henderson, 1973). In contrast *A. gracile* in Fay Lake was found only in shallow water, suggesting that in the presence of fish the shallows provide refuge, as they do for corixid bugs (Macan, 1965), *Bufo* and *Rana* tadpoles (Macan, 1966), and mosquito fish *Gambusia* (Goodyear, 1973). The overrepresentation of flight toward shore, into even shallower water, and the reduced tendency to burrow as depth decreased further indicate that shallows are a refuge. Animals in the deeper parts of the inhabited area were most likely to seek the alternative refuge of burrowing into the substrate.

While flight behavior was almost completely different in the two populations, there were two similarities: the tendency to orient toward deep water and the consistent under-representation of the lateral alternative (*i.e.,* perpendicular to the shore-deep water axis) in all components of the flight behavior sequence. These behaviors, particularly the tendency to turn to flee if oriented laterally, suggest a geometry of flight behavior based on predator behavior. Terrestrial predators, other than diving birds, would approach from shore; fish were almost always seen in deep water, thus their forays toward the shallows would most commonly be toward shore. Salamanders positioned or moving perpendicular to the shore-deep water axis would subtend a larger angle of perception by a predator in deeper or shallower water than would animals aligned with or moving along the axis. Salamanders oriented with the shore-deep water axis would thus suffer less risk of detection. This was quite noticeable in my own "predatory" searches: salamanders broadside to my approach could be seen from a distance often exceeding 1.5 m; animals aligned with my approach often remained undetected until I was directly above them. This effect was especially marked in patches of *Isoetes*. Animals fleeing along the axis would be less likely to attract attention of another predator in deep water or near shore, thus avoiding the predator-

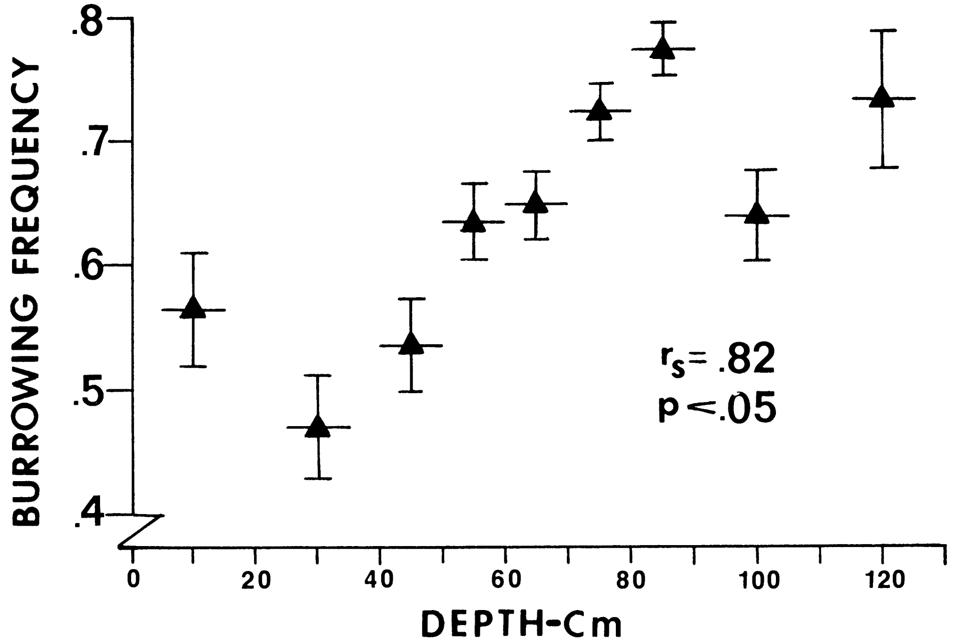

Fig. 3. — Relationship between depth and frequency of burrowing in the substrate at the end of the escape movement. Spearman rank correlation coefficient is represented by r_s. Vertical bars represent 2 SD

enhancement effect noted by Charnov *et al.* (1976). Curio (1976) presents evidence that predators may base their attack path on a prey's head-tail orientation. The converse, that prey may key on predator directionality, must be considered.

The shore-deep water axis has been referred to as the "Y-axis" by several workers who have demonstrated in the laboratory that anurans (Ferguson, 1963; Ferguson and Landreth, 1966; Goodyear and Altig, 1971) and salamanders (Landreth and Ferguson, 1967; Tomson and Ferguson, 1972; D. Taylor, 1972) orient along the axis when exposed to celestial cues. Larval *Ambystoma tigrinum* (D. Taylor, 1972), *A. opacum, A. maculatum* and *A. talpoideum* (Tomson and Ferguson, 1972) move toward deep water in choice experiments; the orientation reverses 180° at metamorphosis. Tomson and Ferguson (1972) suggested that larval orientation toward deep water is a response to predators in the shallows. The behavior of Dark Lake salamanders supports that hypothesis. The tendency of Fay Lake salamanders to escape toward shore and the depth-specific movements of large salamanders demonstrate plasticity of the behavior. My results confirm orientation behavior in field populations, though the pertinent orientation cues are unknown. Animals in the laboratory experiments used celestial cues and were generally unable to orient on cloudy days. Salamanders in the field should orient whenever active if the behavior is advantageous; perhaps they cue on the slope of the bottom.

Hedberg (1981) demonstrated a possible stress-warning marker in *Ambystoma tigrinum,* though he could only speculate about the origin or function of this marker. If there are specific behaviors that enhance successful escape from a predator, as suggested by my study, then the ability to detect stress of conspecifics and prepare to undertake the appropriate flight behavior should have high selective value.

Flight behavior was nonrandom in both lakes. The question then arises, why don't predators take advantage of this by learning to anticipate the more common sequences? While some alternatives were more common than predicted by random expectation, they were not the most common on an absolute basis. Lateral escape, the most underrepresented alternative when compared to random expectation, was actually the most common movement in every case but one. Thus, in a given attack a predator would be most likely to experience lateral flight, providing no information about the nonrandomness of response in the population. The nonrandom behaviors do not minimize diversity of behavior; they overlie the diversity. Diversity of flight behavior should prevent counterlearning by predators (Schall and Pianka, 1980). Although nonrandom behavior is present, the overall effect is protean (Chance and Russell, 1959) in that predictability of a single individual's behavior is low.

There may be a component of learning in the flight behaviors, though as Schall and Pianka (1980) point out, observations on flight are often consistent with both evolutionary and learning hypotheses. First, the behaviors are diverse, with nonrandom behavior emerging only from the context of random expectation. This would be expected if there were two types of behavior in a population: the essentially random behavior of naive animals, not yet subjected to attack, overlaid by nonrandom behavior of experienced animals that always responded with the same behavior that had brought them refuge from a previous attack. Second, the nonrandomness of flight behavior of Fay Lake salamanders was much more intensively developed in the large (oldest) size class than in smaller (younger) animals; direction of flight was dependent on depth in large animals only. Though natural selection or an ontogenetic effect cannot be ruled out, the large size class should have had more experience with predators, with more reinforcement of flight to refuge and more opportunity to associate a particular depth with a particular escape. Finally, the Fay Lake salamanders had been exposed to trout predators for only about 25 years (J. Griggs, Oregon Fish Commission, pers. comm.). The differences between the Fay and Dark Lake populations are much better explained in terms of behavioral plasticity directed by differential predation than by evolution of behavior in a short period of time.

Burger (1950) observed the extinction of neotenic *Ambystoma tigrinum nebulosum* in Emerald Lake, Colorado, after the introduction of trout. Sprules (1974) found that this subspecies never occurred in a neotenic form in lakes into which trout had been introduced, though neotenes were present in adjacent fishless lakes. Conant (1975) notes that larval *A. t. tigrinum* are "common in farm ponds—until such ponds are stocked with fish!" Why does neotenic *A. gracile* persist when trout are introduced, when neotenic *A. tigrinum* becomes extinct? Does the answer lie in the plasticity of behavior of *A. gracile?* Persistence of *A. gracile* in Fay Lake is obviously related to refuge in the shallows, but the very presence of nonrandom orientation and flight, particularly the depth-specific movements, suggests that they enhance the physical refuge.

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