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THE STUDY OF ANTIPREDATOR BEHAVIORS OF FORMOSAN SALAMANDERS (*HYNOBIUS FORMOSANUS*)[1]

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K. C. Kant Yeh, Kuo-Shou Chuang, Kuang-Yang Lue and Shyh-Hwang Chen (1988) The study of antipredator behaviors of Formosan salamanders (*Hynobius formosanus*). *Bull. Inst. Zool., Academia Sinica* **27**(1): 37-48. Antipredator behaviors of Formosan salamanders (*Hynobius formosanus*) were studied. Total 13 behavioral patterns were observed, i. e. tail arched, tail elevated, tail undulated, tail coiled, tail lashed, tail wagged, body arched, body elevated, body coiled, thrush in running motion, avoidance, retreat and immobility. Among these, tail-lashed and avoidance showed the highest frequencies. Behavioral diversity index was calculated by the information theory for understanding their evolutionary differentiation on behavioral patterns. The index was higher in juveniles than mature animals. The constructed phenogram indicated that two groups of behavioral patterns were clearly separated. The dominant one is corresponded with Brodie's suite II—Tail lashing. Data analysis on scars of tail parts, showed that the opportunities for mature animals to have scars were much higher than immature ones. Scars caused by predation, courtship fighting and other reasons were discussed very detail in the report.

Key words: *Hynobius formosanus*, Antipredator behavior, Information theory, Cluster analysis, Biting scars.

Most animals, including amphibians, more or less have special morphological structures or antipredator behaviors to avoid being preyed by other animals. Various groups of salamanders, including Hynobiidae, Ambystomtidae, Salamandridae and Plethodontidae are usually terrestrial and naturally face the predation by many predators. In response to these predation pressures, many salamanders have evolved independently several antipredator mechanisms. In behavioral adaptations, biting, vocalization (Brodie, 1978), rib penetration (Nowak and Brodie, 1978), escaping, immobility and posturing were frequently observed.

Recently antipredator behaviors of salamanders were intensively studied by Brodie (1968, 1977, 1978, 1982 and 1983). The salamanders he tested or observed were mostly from new world. Only few species of salamanders from East Asia were described. *Hynobius formosanus*, an endemic relic species of the last glacial period, distributes over high mountain areas, which are mostly 2000 m above sea level, in remote regions of Taiwan. Its population is very small. Basic information and relative research about this species are very limited (Chen *et al.*, 1986a, 1986b).

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The aim of this study is to understand the antipredator behaviors of Formosan salamanders, and to clarify the differences between related species which inhabit in other countries. Meanwhile, we try to investigate the strategies of antipredater behaviors and the predation phenomena of this species. Besides, the relationships among all behaviors recorded were tested by several statistics methods to find out the relationships among them.

MATERIALS AND METHODS

The antipredator behavioral patterns (ABPs for short) of *Hypnobius formosanus* were tested by using Brodie's method (1977, 1983). Animals collected from fields of 20 localities (Table 1) were kept in a temperature-controlled environmental chamber at 10°C–15°C. All ABPs were recorded from 81 individuals by using a pincer (Brodie, 1977) or finger as a stimulant. For understanding the evolutionary information content and variability of behavior in each group, the information theory was used. The behavioral index ($D(i)$) of the group is calculated with the following modified formula:

$$D(_i) = -\sum_{k=1}^{n} p\ (k_i) \log_2 p(k_i)$$

where i represents the ith age group, k the various behaviors in each group and $p(k_i)$ the probability of the behavior k of the ith group.

The relationships of ABPs among various age groups were analyzed by using contingency tables method. The similarities among various beavioral patterns were evaluated. The index of similarity (IS) is also calculated by using following formula. For linkage procedure, use UPGMA algorithm to compute the average similarity of a candidate OTU to an extant cluster (Sneath *et al.*, 1973).

TABLE 1

Twenty localities of Formosan salamanders, *Hynobius formosanus* examined for ABPs

Locality	No. examined
1. Alishan (阿里山)	11
2. Shang-yang section of S. E-W crossed high way (南横向陽路段)	8
3. Shang-yang shelter of S. E-W crossed high way (南横向陽小屋)	2
4. Bee-lu (畢祿)	5
5. Ho-huan (合歡)	5
6. Nan-hoo (南湖)	4
7. Nan-hoo creek (南湖溪)	2
8. Nan-hoo south peek (南湖南峯)	2
9. Nan-hoo creek head source (南湖溪源頭)	4
10. Chung-yan jen creek (中央尖溪)	1
11. Tian pool (天池)	6
12. Pa-tung-kuan (八通關)	2
13. Pei-miann creek (北面溪)	4
14. Lao-long creek (荖濃溪)	1
15. Yun-hae (雲海)	3
16. Dan-dah shan (丹大山)	4
17. Tay-pyng creek (太平溪)	3
18. Neng-kao shan (能高山)	2
19. Lha-kuhin creek (拉庫音溪)	4
20. Chi-lai north peek (奇萊北峯)	8
Total	81

$IS = [N_{ij}/(N_i + N_j - N_{ij})] \times 100\%$

N_{ij}: number of occurred behavioral pattern i and j simultaneously

N_i: number of occurred behavioral pattern i

N_j: number of occurred behavioral pattern j

To understand the possible predation pressures in nature, we also recorded the biting scars on tail part, and tested the difference among three age groups of 130 preserved specimens by using Chi-square Contingency tables menthod.

III. RESULTS

Thirteen ABPs were observed from Formosan salamanders (Table 2), accoording to Brodie's (1982, 1983) descriptions:

Tail arched (TA)—The midpoint of the tail is higher than either the proximal or distal end. (Fig. 1, 2)

Tail elevated (TE)—The distal portion of the tail is raised higher than any part. (Fig. 3, 4)

Tail undulated (TU)—The tail is moved slowly back and forth in a serpentine manner; it is usually associated with an arched or elevated tail. (Fig. 5)

Tail coiled (TC)—The tail is usually tight with the base of the tail. (Fig. 6)

Tail lashed (TL)—The tail whips to right and left vigorously. (Fig. 7, 8)

Tail wagged (TW)—The tail is raised off the substratum, held straight and swung from side to side.

Body arched (BA)—The midpoint of body is elevated off the substratum and is higher than the pelvic or pectoral region.

Body elevated (BE)—The body is raised off the ground by stiffening the front, rear, or all four limbs.

Body coiled (BC)—Coiling is usually tight with the head near the base of the tail. The limbs and the tail may or may not be coiled around the body. (Fig. 8)

Thrush in running motion (TH)—The animal walks quickly as swimming in the water. (Fig. 9)

TABLE 2
Frequencies of 13 antipredator behavioral patterns among three age groups of Formosan salamanders

Group	0-2.5 cm		2.5-4.5 cm		>4.5 cm		Total	
n	4		9		68		81	
ABPs	f	%	f	%	f	%	f	%
Tail arched	3	75.0	5	55.6	44	64.7	52	64.2
Tail elevated	4	100.0	4	44.4	22	32.4	30	37.0
Tail lashed	4	100.0	8	88.9	46	67.6	58	71.6
Tail undulated	2	50.0	5	55.6	18	26.5	25	30.9
Tail wagged	1	25.0	4	44.4	13	19.1	18	22.2
Tail coiled	2	50.0	1	11.1	10	14.7	13	16.0
Body arched	1	25.0	0	0.0	8	11.8	9	11.1
Body elevated	0	0.0	1	11.1	0	0.0	1	1.2
Body coiled	1	25.0	3	33.3	17	25.0	21	25.9
Thrush	2	50.0	2	22.2	25	36.8	29	35.8
Immobility	0	0.0	0	0.0	1	1.5	1	1.2
Avoidance	3	75.0	4	44.4	49	72.1	56	69.1
Retreat	3	75.0	4	44.4	32	47.1	39	48.1

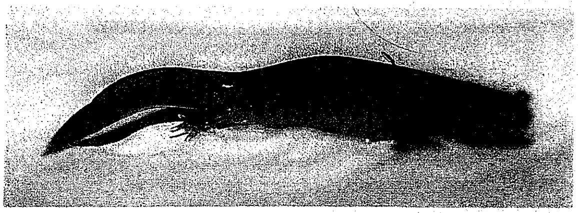


Fig. 1. Low intensity in Tail-arched in *Hynobius formosanus* from Southern E-W crossed high way.

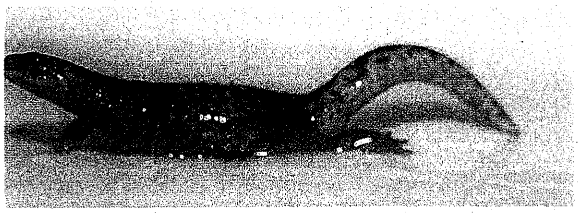


Fig. 2. High intensity in Tail-arched in *Hynobius formosanus* from Chung-yan jen creek.

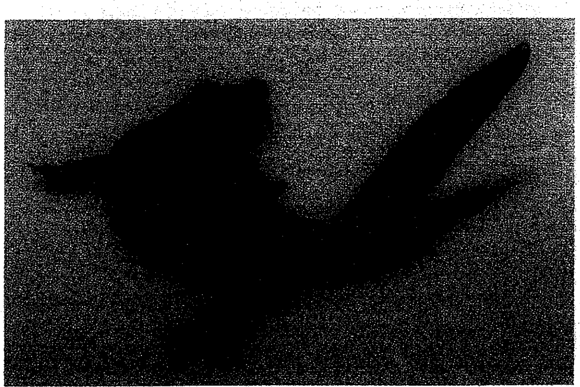


Fig. 3. Tail-elevated posture in *Hynobius formosanus* from Nan-hoo area.

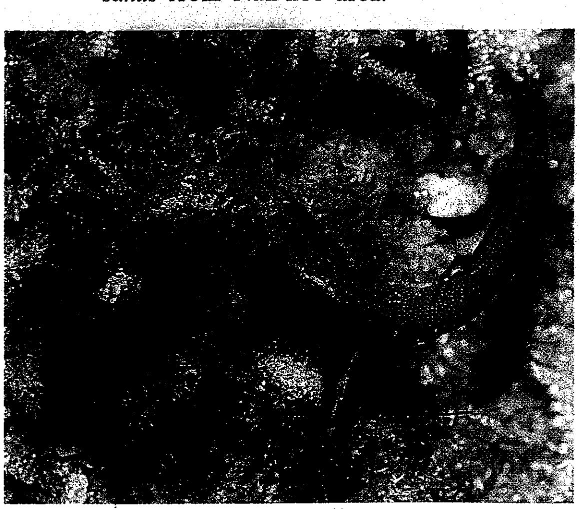


Fig. 4. Tail-elevated posture in *Hynobius formosanus* from Alishan.

Fig. 5. Tail-undulated posture in *Hynobius formosanus* from Alishan.

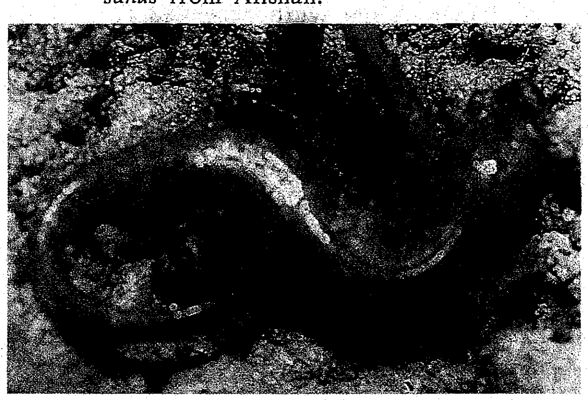


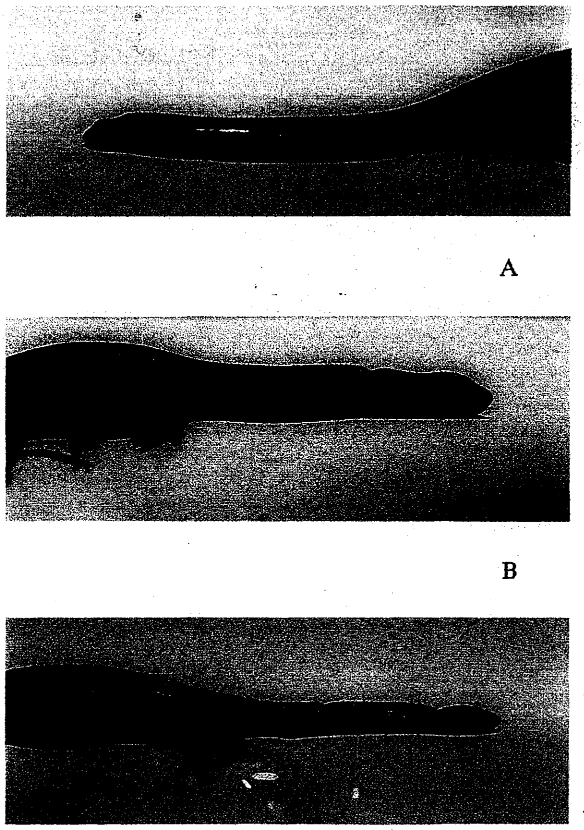
Fig. 6. Tail-coiled posture in *Hynobius formosanus* from Alishan.

Fig. 7. Tail-lashed posture in *Hynobius formosanus* from Alishan.

Fig. 8. Body-coiled and Tail-lashed displays in *Hynobius formosanus* from Alishan.

Fig. 9. Thrush in running motion of *Hynobius formosanus* from Ho-huan area.

Fig. 10. Avoidance posture in *Hynobius formosanus* from Alishan.



A

B

C

Fig. 11. Biting scars on tail parts in *Hynobius formosanus.* A, B from Nan-hoo area, C from Southern E-W crossed high way.

TABLE 3
Frequencies and behavior diversity indices of 13 antipredator behavioral patterns among three age groups of Formosan salamanders

Age classes	0-2.5 cm	2.5-4.5 cm	>4.5 cm
n	4	9	68
Sum	26	41	285
Ave	6.50	4.56	4.19
$D(i)$	3.305646	3.260622	3.265366

Avoidance (AV) — The animal moves away from the direction of the stimulus. (Fig. 10)

Retreat (RE)—The animal move backward.

Immobility (IM)—This is a type of freezing behavior.

Among 13 dehavioral patterns observed, TAIL-LASHED (f=58), AVOIDANCE (f=56) and TAIL-ARCHED (f=52) showed with the higher frequencies (at frequency level>60% per sample in Table 2), BODY-ELEVATED and IMMOBILITY with the lower frequencies (rare patterns at frequency level <10% per sample).

We summed them up and averaged frequencies of 3 age classes except the behavioral pattern of IMMOBILITY (Table 3). Results indicated that the small animal has higher response rate than the older one. First, the average of the behavioral frequency of younger individuals is higher than those of older ones, i. e, 6.5 (S. V. <2.5 cm)< 4.56 (S. V. 2.5-4.5 cm)>4.19 (S. V, >4.5 cm). Second, the behavioral diversity index of youngest group is the largest one among three age groups (Table 3).

In the analysis of contingency tables, behavioral patterns and age classes are independently distributed within individual samples for all, except two comparisons (Table 4). The two exceptions were TAIL-ELEVATED behavior vs. age group (p<0.25, smaller individuals tend to have higher response rates of TAIL-ELEVATED behavior than larger ones) and BODY-ELEVATED vs. age group. Although significance level of chi-square in BODY-ELEVATED vs. age group is less than 0.02, yet the response rate is very small (sum=1).

TABLE 4
Difference in 13 antipredator behavioral patterns among three age groups of Formosan salamanders

Behavior Pattern	Chi-squares	Significant
Tail arched	0.50317	0.7726
Tail elevated	7.65156	0.0218*
Tail lashed	3.43245	0.1797
Tail undulated	3.87303	0.1442
Tail wagged	2.96849	0.2267
Tail coiled	3.67594	0.1591
Body arched	1.93566	0.3799
Body elevated	8.10000	0.0174*
Body coiled	0.28929	0.8653
Thrush	1.10034	0.5769
Immobility	0.19357	0.9078
Avoidance	2.90817	0.2336
Retreat	1.23699	0.5388

d. f.=2, *: 95% significant

Thirteen behavioral patterns in similarity dendrogram can be divided into two subsets (Fig. 12). The first subset (including TAIL-ARCHED, TAIL-ELEVATED, TAIL-LASHED, TAIL-UNDULATED, TAIL-COILED, BODY-COILED, THRUSH, AVOIDANCE and RETREAT) represents an ordinary way to avoid being attacked. The other subset, a special way in response to enemy's attack, represents a sort of defending strategy. Animals with the second subset postures of

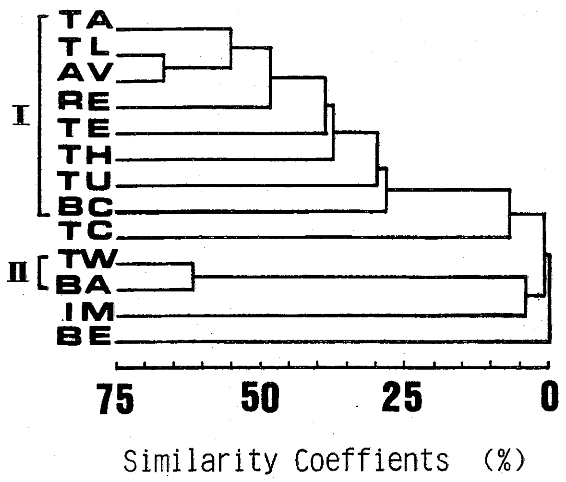


Fig. 12. Dendrogram of 13 antipredator behavioral patterns in Formosan salamanders.

elevating-body and wagging-tail, do not escape or retreat.

According to S. V. length (Snout-Vent), salamanders could be separated into three age classes (Table 7) (Chen *et al.*, 1986a). Total 130 preserved animals were examined. Within 95 individuals with S. V.$>$4.5 cm 36 had abnormal tails; 19 with S. V. 2.5–4.5 cm 2 were abnormal. All 16 animals with S. V. $<$2.5 cm were normal. By Chi-square calculation ($p<0.01$), the result showed that the frequency of scars increased with age of the salamanders.

DISCUSSION

Prior to this research the endemic Formosan salamander had not been studied on the topic of antipredator display. Only few papers referred to the research history, taxonomy and population estimation on *Hynobius formosanus* (Chen *et al.*, 1986a, 1986b).

Brodie (1983) listed 24 antipredator mechanisms in terrestrial salamanders and concluded 4 common suites of correlated antipredator mechanisms that act synergistically to increase the protection on salamanders. The 4 common sets include unken reflex, tail lashing, tail undulation and head butting, all evolved from a common hypothetical ancestral condition. The antipredator adaptations of salamonders interact in a "synergistic" manner.

By comparing with the displays listed by Brodie's (1983), the antipredator displays in salamanders' populations of Taiwan seem to be simpler than other investigations by showing less behavioral patterns. We suspect that the populations, as *Hynobius formosanus*, face fewer predators and display plainer postures than other species not living in such remote and isolated conditions. From our data in Table 2, the exhibition of tail lashing shows the highest rate among all ABPs. We supposed that *Hynobius formosanus* belongs to Brodie's second suite (Tail lashing). The result in Fig. 12 also indicated that *Hynobius formosanus* reveals typical tail-lashing suite characteristic.

By examining the data in Table 3, we can point out that the younger individuals are more active than mature ones when attacked by the pincer. Results (Table 3) reveal that the younger individuals display more actively and have a higher behavioral diversity index (variability) than the older ones. Information theory was primarily applied in estimation of species diversity (Krebs, 1985). It was also used in estimation of the information content and variability, diversity index, of a series of behaviors (or among individuals) (Huntingford, 1984). We modify the original formula into the formula stated in Method for understanding the data structure of all behaviors in each experimental age group. According to the behavioral diversity index of Table 3, the juvenile group has the higher value than the older ones. The younger individuals possess more variability in behavioral display than older ones. It means that animals will not show or will lose certain antipredator behaviors in the process of individual developments. It is reasonable because of predation pressures in mature individual will be much less than in juvenile ones. Besides, adult animals are well in morphological and physiological aspects to fit their environments or even to combat with predators.

Although the result on Table 4 by using contingency tables method revealing TAIL-ELEVATED vs. age graoup and BODY-ELEVATED vs. age group estimations are dependently distributed within individual samples, yet it is not enough to explain that there is no difference in other behavior displays. In discussion on behavioral difference, several conditions must be intended (Huntingford, 1984), such as morphological variables (body size, litter size, etc.), unsuitable environments, sex ratio of the group, phylogenetic factors, etc. It is difficult to explain well on all behavioral mechanisms, because they may be affected by many distresses. Besides, different individuals may have diverse differentiation in behaviors. Ducey *et al.* (1983) stated that salamanders do show different antipredator behavial patterns when defferent types of contacts with garter snakes were conducted. Individuals display the

TABLE 5

Number of individuals occurred any two antipredator behavioral patterns simultaneously in Formosan salamanders

	TA	TE	TL	TU	TW	TC	BA	BE	BC	TH	IM	AV	RE
TA	—	21	32	15	0	6	0	0	14	19	0	33	25
TE		—	20	9	0	1	0	0	8	13	0	18	14
TL			—	18	10	4	7	0	12	20	0	38	24
TU				—	0	2	0	0	8	9	0	17	14
TW					—	0	8	0	1	4	1	9	0
TC						—	0	0	1	4	0	7	7
BA							—	0	0	2	0	7	0
BE								—	0	0	0	0	0
BC									—	9	0	14	9
TH										—	0	18	15
IM											—	0	0
AV												—	27
RE													—

TABLE 6

Matrix of similarity coefficients between any two antipredator behavioral patterns of Formosan salamanders

	TA	TE	TL	TU	TW	TC	BA	BE	BC	TH	IM	AV	RE
TA	—	46.7	55.2	31.9	0.0	12.5	0.0	0.0	29.8	38.0	0.0	55.0	49.0
TE		—	41.7	29.0	0.0	3.2	0.0	0.0	25.8	38.2	0.0	34.0	35.0
TL			—	39.1	20.4	7.7	14.9	0.0	23.5	39.2	0.0	66.7	44.4
TU				—	0.0	7.7	0.0	0.0	29.6	26.5	0.0	34.0	38.9
TW					—	0.0	61.5	0.0	3.4	11.8	7.7	17.0	0.0
TC						—	0.0	0.0	3.8	12.9	0.0	13.5	20.0
BA							—	0.0	0.0	6.5	0.0	14.0	0.0
BE								—	0.0	0.0	0.0	0.0	0.0
BC									—	27.3	0.0	26.9	22.5
TH										—	0.0	32.1	35.7
IM											—	0.0	0.0
AV												—	50.0
RE													—

species those typical behavior should be higher than those exhibiting the atypical behavior.

Duellman and Trueb (1986) stated that some similarities exist between the behaviors of salamanders and anurans, but they thought the differences and unique attributes of each group are sufficient so that each group is best to treated individually. Behavioral similarity analysis (Table 5, 6) in this study is a tool to evaluate the closest relationship between any two patterns. Cluster analysis methods were widely applied in quantitative ethology (De Ghett, 1978; Schnell *et al.*, 1983), and the hierarchical cluster analysis (Wiepkema, 1961; Morgan *et al.*, 1976) was recommended as an excellent method for ethologist to check out the structure of various behavioral categories. The phenogram of Fig. 12 indicated that two groups of patterns were clearly separated, the dominant one is corresponded with Brodie's SUIT II—Tail-lashing.

De Ghett (1978) cautiously pointed out that various types of behavioural problems might occur by using cluster analysis. He suggested that ethologists should be careful in explaining the result of cluster analysis, even by other statistical methods. Sometimes, detail explanations on the data of cluster analysis will misunderstand the real relationships among those ABPs. It is worthy to establish the hierarchical structure among behaviors by cluster analysis method. As discussed abve, among animals the the behavioral variations do exit (Ducey *et al.*, 1983), the species-typical behavior would be display more frequently than atypical one. So that result from the preliminary analysis of this paper were corresponded to Brodie's suggestion that *Hynobius formosanus* can fit into Suit II (Tail-lashing), because tail-lashed pattern displayed by experimental animals showed most dominantly among all behavioral patterns, and was the first synthetic cluster (with Avoidance) in Fig. 12.

In his reports (1977, 1982 and 1983), Brodie mentioned that *Hynobius* possess seven following antipredator mechanisms to detract predators.

(1) noxious skin secretion
(2) glandular tail dorsum
(3) glandular tail venter
(4) aposematic coloration on dorsum
(5) body coiled
(6) tail lashed
(7) tail wagged

In 1982, Brodie only pointed out *Hynobius* displays four antipredator characteristics—(1), (2), (4) and (7), while in 1983, he listed all above seven characteristics. In our study, *Hynobius formosanus* showed not only body coiled, tail lashed and and tail wagged but also did other ABPs, listed in Table 2. As Brodie's Suite II (tail lashing), among 13 ABPs of *Hynobius formosanus* tail lashed occurs most ferquently.

In Hynobiidae, glandular glands distribute all over the body especially on the tail part. Among ABPs related to tail movements, they were discussed very detail by Brodie and his colleagues (Brodie, 1977) such as tail arched, tail lashed, tail wagged, tail undulated, and tail coiled. They discovered that the tail is used to attract predators in these behaviors. Under most circumstances, salamanders will use the tail to attract, and the predator will attack the tail part first. The attack sometimes will leave the scars on the tail when it is unsuccessful. Glands on the tail part secrete noxious substances (Brodie, 1982), which cause an unpleasant feeling to the predators and lead them to release the prey. There is no reason to doubt that the unsuccessful predation is caused by these noxious substances. The skin secretion of *Hynobius formosanus* did cause an unpleasant feeling to authors.

During the experiments, individuals with scars (Fig. 11) on tail were discovered frequently. If the abnormality on the tail part was caused by the genetic deficiency, then there should be no great difference among various age grounps. We assume that this phenomenon about scars of the tail was caused from the unsuccessful predation by predators (including the larger individuals

TABLE 7
Biting scars records from various age groups of salamanders examined

	Small	Medium	Large	Total
with scale	0 (4.7)	2 (5.6)	36 (27.8)	38
normal	16 (11.3)	17 (13.4)	59 (67.2)	92
Total	16	19	95	130

Contingency tables, chi-square=13.2693***

of the same species). Results obtained from Chi-square analysis (Table 7) showed that this deficiency rate is associated with the age of individuals. The number of records in adult with scar is much higher than the juvenile age group. It is reasonable to believe that the older individuals escape more from unsuccessful predations than the younger ones, naturally these will leave more biting scars on the tail. In another aspects, the total chances for juveniles coming across with the predators are much less than the adults.

Scars might be left by fighting between individuals besides the unsuccessful predation mentioned above. In fields we did not see any fighting and cannibalism within Formsan salamanders. One case of cannibalism was observed in environmental chamber in 1983. It is reasonable to believe that fighting including the courtship competition and cannibalism will occur in fields, and leave scars on the tail part of this species.

Birds (thrush) (Brodie, Jr. and Brodie, III, 1980; Brodie and Howard, 1973), snakes (Ducey *et al.*, 1983), small mammals and shrews (Brodie *et al.*, 1979) are the main predators for salamanders in fields. There is no report about predators for Formosan salamanders in Taiwan. In 1982, three adult salemanders were discovered from the stomach of a snake (*Pseudoxenodor macropus stejnergeri*), near Ta-wu shan, 2500 m abov the sea level. All three were longer than 4.5 cm in S. V. length. Surprisingly, one salamanders had two scars on the tail. Besides, Mikado pheasant, small rodents (*Rattus* and *Apodemus*) and Blind mole (*Mogera insularis*) were found in several localities, where salamanders were discovered. It is reasonable to believe that these animals are predators for *Hynoius formosanus* (Table 8).

The antipredator mechanisms associated the colorations may also be important for salmandes to survive. Brodie and Howard (1972) described that the behavioral mimicry in defensive displiays in two urodele amphibians is associated with the coloration patterns. There are three distinct color patterns in *Hynobius formosanus*, brown type, black-gray type and orange type (Chen *et al.*, 1986a). These different colorations might team up with ecological reasons to enhance their survivals. The relationship between colorations and antipredator mechanisms of *Hynobius formosanus* is a topic worth to investigate.

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TABLE 8
The possible natural predator for Formosan salamanders

1. Snake. —Three dead salamanders were found in the stomach of *Pseudoxendon macropus stejnergeri.*
2. Birds. —Mikado pheasant (*Syrmaticus mikado*) was found in one location where salamanders were collected.
3. Mammals.—Formosan blind mole (*Mogera insularis*) and Chinese mink (*Mustela sibrica davidiana*) were found in some locations where salamanders were collected.

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臺灣山椒魚 (*Hynobius formosanus*) 之禦敵行爲研究

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本研究係對臺灣山椒魚 (*Hynobius formosanus*) 進行禦敵行爲態式之探討，共記錄到尾部拱起 (tail-arched)、尾部舉起 (tail-elevated)、尾部波浪狀擺動 (tail-undulated)、尾部捲屈 (tail-coiled)、尾部掃動 (tail-lashed)、尾部擺動 (tail-wagged)、身體拱起 (body-arched)、身體舉起 (body-elevated)、身體捲屈 (body-coiled)、衝撞 (thrush in running motion)、逃避 (avoidance)、後退 (retreat) 及不動 (immobility) 等十三種不同行爲態式。其中以尾部掃動及逃避之出現頻率最高。利用 Information Theory 所測得之各年齡組內行爲歧異度及平均頻度顯示該等數值以幼齡組羣較成年組羣來得高。利用聚團矩陣分析法 (Cluster analysis) 來探討各行爲之層次相關性所得樹枝圖，明顯地可以將行爲態式分爲二羣。優勢羣則符合 Brodie 之第二分類羣——尾部掃動。有關尾部缺刻情形，利用 Chi-square 分析結果亦顯示年齡組羣間有顯著之差異；以成熟個體顯示有較多的缺刻。推測缺刻傷痕之造成原因可能是被捕食、打鬬及其它原因，這些在文中都有詳細討論。