

The different Polyphenism by the Level of Predation Risk and Habitat in Larval Salamander, *Hynobius ieechii*¹

Ji-Hee Hwang², Hoon Chung^{3*}

한국산 도롱뇽의 포식압과 서식지에 따른 polyphenism¹

황지희² · 정훈^{3*}

ABSTRACT

This study examined the different polyphenism of larval salamander *Hynobius ieechii* according to two habitats, pond and stream. We collected salamander's eggs from three regions including Mountain Inwang, Surak and Gwangju. Eggs were treated by four different conditions according to predation level and habitat: high risk - which had a predation risk three times a day; low risk - which had no predation risk, pond and stream habitat. Predation risk was conducted by using chemical cue from Chinese minnows. The chemical cue treatment started from the day of collection and ended one week after the hatching. After the treatment phase, we measured the head width at the level of the eyes(HWE) and the largest head width(LHW) and snout-vent length of the each larva. We calculated the ratio of the head size by dividing HWE by LHW and made a comparison with each of the average ratio of head size according to the predation risk. The results showed that there was a significant difference in the ratio of the head size and snout-vent length according to the predation risk and habitat. From these results we found that predation risk and habitat condition can cause the different polyphenism to the larval salamander and these morphological changes could be affect their mortality.

KEY WORDS: KOREAN SALAMANDER, CANNIBALISM, CHEMICAL CUE, SALAMANDER LARVAE, CANNIBAL MORPH

요 약

본 연구는 서식지와 포식압에 따라 머리 크기가 서로 다르게 나타나는 polyphenism에 대하여 한국산 도롱뇽 유생을 대상으로 이루어졌다. 인왕산과 수락산, 경기도 광주에서 채집해 온 도롱뇽의 알(난괴)을 서식지 특성과 포식압에 따라 4가지 그룹으로 나누었다. 서식지는 계곡 형과 웅덩이 형 두 그룹으로 나누었고, 포식압은 높음과 포식압 없음, 두 그룹으로 나누었다. 포식압 수준은 하루에 포식자의 cue에 노출된 빈도로 나누었으며 높은 수준은 하루 세 번으로 하였다. 포식 cue는 버들치의 냄새를 추출하여 사용하였고, 알 채집일 다음날부터 부화 후 일주일까지 cue에 노출 시켰다. Chemical cue 노출 처리가 끝나는 부화 후 일주일일이 되는 날, 각 도롱뇽 유생의 머리 중 가장 넓은 부분과 눈이 있는 부분의 길이, 그리고 snout-vent length를 측정하였다. 눈이 있는 부분의 길이는 머리 중 가장 넓은 부분으로

1 접수 2010년 10월 31일, 수정(1차: 2010년 12월 21일), 게재확정 2010년 12월 22일

Received 31 October 2010; Revised(1st: 21 December 2010); Accepted 22 December 2010

2 삼육대학교 대학원 생명산업학과 행동과학연구실 Department of Bioindustry, Sahmyook University, Seoul(139-742), Korea(clxkh86@nate.com)

3 삼육대학교 동물과학부 Department of Animal Science, Sahmyook University, Seoul(139-742), Korea(chungh@syu.ac.kr)

* 교신저자 Corresponding author(chungh@syu.ac.kr)

나눈 수치를 이용하여 통계 처리를 하였으며 결과는 다음과 같다. 도롱뇽 유생의 머리 크기 비율은 포식압의 수준이 높음에 따라 의미 있게 증가하였다. 또한 계곡형 서식지에 사는 도롱뇽 유생의 머리는 버들치의 cue에 반응하여 포식압이 높을 때 머리 크기 비율이 의미 있게 증가하지만, 웅덩이형 서식지에 사는 도롱뇽 유생은 무의미한 결과가 나타났다. 그리고 snout-vent length의 길이는 서식지와 상관없이 높은 포식압에서 증가하는 경향이 나타났다.

주요어: 한국산 도롱뇽, 동중포식, chemical cue, 포식압, 도롱뇽 유생

INTRODUCTION

Amphibians are found in humid microhabitat and have inhabited from the valleys on highlands to low hill districts, plane or near the house. In general, Korean salamander, *Hynobius ieechii*, is living at the humid soil like around the tree roots or wetlands(Yang *et al.*, 2001). To be specific, Larval Korean salamanders are usually found at the small pond which generated by the water flowed from the upper side. But sometimes they are found in the small valley where the water always flows. Therefore, each habitat has different environmental circumstance and the main predator should be differed from each other. Because even changes in hydroperiod are changes in predators(McPeck, 1990a; 1990b; Welborn *et al.*, 1996; Skelly, 1997) and variation in hydroperiod and predators creates different selective forces for organisms in ponds from different positions along the gradient(Richardson, 2001). Many aspects of salamander phenotypes are potentially flexible (Buskirk and Schmidt, 2000), we assumed the habitat as a important phenotype inducing factor.

Polyphenism is the occurrence in a population of alternative phenotype that are produced from a single genotype in response to different environmental stimuli (West-Eberhard, 1989). Such adaptive plastic responses should improve an individual's fitness relative to those exhibiting nonplastic traits(Schlichtign and Pigliucci, 1998). It often results in expression of the phenotype most advantageous under current environmental conditions, thereby facilitating an examination of the fitness consequences of different phenotype(West-Eberhard, 1992).

There are many factors which affecting their morphology and life history. However, we would like to focus on the predation risk, chemical cue, because the level of perceived predation risk under natural conditions can vary over time due to seasonal changes in local predator and/or

prey guild membership, prey movements through heterogeneous microhabitats, and/or movement of potential predators(Sih *et al.*, 2000; Brown *et al.*, 2006). As many studies found out that chemical cue plays a large role in shaping the phenotypic traits of aquatic organisms, the growing recognition about it has important implications for the study of aquatic food webs(Turner *et al.*, 2000).

Aquatic animals are using chemical information from the environment for behavioral decision making relating to foraging, reproduction and the assessment of predation risk(Wisenden, 2000). Predation events escalate along a series of steps beginning with initial detections leading to attack, capture and finally to prey ingestion(Lima and Dill, 1990). At each step in this 'predation sequence' chemical cues are released that can be used by prey to assess and avoid predation risk. In response to these cues, prey adopts species-specific antipredator behaviour. Typically, these involve any or all of the following: reduction in activity, movement out of the water column, seeking shelter, area avoidance, increased shoal cohesion(Wisenden, 2000), and changing morphology(Kats and Dill, 1998; Tollrian and Harvell, 1999).

In particular, the presence of discrete phenotypic differences in behavior, morphology and life history among individuals of a species in relation to cannibalism is known as "cannibalistic polyphenism" (Polis, 1981; Crump, 1992). Cannibalism is a phenomenon ingesting of all or part of a conspecific which occurs in nearly every major vertebrate and invertebrate group(Elgar and Crespi, 1992). In some species, certain individuals even develop specialized weaponry to facilitate the capture and consumption of conspecifics.

For example, tiger salamander larvae(*Ambystoma tigrinum*) occur in nature as two alternative morphs: a typical morph that feeds mostly on invertebrate prey and a cannibal morph that has a wider gape, enlarged teeth

and modified oral bones to facilitate the ingestion of conspecifics(Pfenning, 1997). One of the studies which researched about the cannibalistic phenotype of larval salamander, *Hynobius retardatus*, used a unique value that measured its head size proportion to evaluate their phenotype numerically.

Wakahara(2001) measured each salamander's head width at the level of the eyes(HWE) and the largest head width(LHW) and divided HWE by LHW and analyzed data to found out the correlation ship between head size proportion and cannibalism. And the results said *H. retardatus* larvae tended to show the broad-headed morphs when it was reared in the scarce food level, high density with others and mixed sibling groups(Wakahara, 1995). Though there were no studies about Korean salamander's cannibal morph, there was a study about their cannibalism. *H. leechii* larvae prefer to consume live, weak and small conspecific and they preyed on siblings more often than non-siblings(Park *et al.*, 2005).

In amphibians, both size at and time of metamorphosis have been found to affect later fitness through effects on juvenile survival and adult fecundity(Smith, 1987; Berven, 1990; Scott, 1994; Altwegg and Rayver, 2003). And the broad-headed morphs were induced without actual cannibalism and induced frequently during the prefeeding stage - from just after the hatching to the initial feeding, approximately 5~6 days(Nishihahra, 1996; Michimae and Wakahara, 2001).

In general, phenotypic differences in life-history and morphological traits observed among natural population of among animals reared under experimental conditions may arise from genetic differentiation due to local adaption and drift or from phenotypic plasticity(Stemberger and Gilbert 1987; Jakson and Semlitsch, 1993; Buskirk and Schmidt, 2000; Merila and Crnokrak, 2001). From these empirical facts, we conducted an experiment to know whether predator's chemical cue affect to the snout-vent length and head proportion of larval salamander in laboratory.

We used Chinese minnows as a predator indirectly by extracting their odor. And we made groups of four according to the habitat characteristic and chemical cue exposure. The exposure to the chemical cue was continued until the day after a week from hatching and we measured the head proportion and snout-vent length of each larva to be compared.

MATERIALS AND METHODS

1. Experiment Animal Collection and Environment

Twenty seven of the Korean salamander(*H. ieechii*) egg mass were collected from stream in Inwang(37°35' 58.8" N, 126°58' 03" E), small pond in the Surak(37°40' 58.1" N, 127°03' 46.3" E), and Mountain Gwangju (37°23' 13" N, 127°12' 24" E), between March 4 and April 3, 2010(Table. 1). In general, Korean salamanders lay their eggs at the small pond which generated by the water flowed from the upper side. But in case of Mountain Inwang, thousands of eggs were laid at about 1km long stream located in the small valley with trees. This region has been famous for its mass breeding place by salamanders and frogs near the civic center in every spring. In particular, the salamander eggs were placed in the part of stream where the water flowed slower than other parts of stream or at the center of the stream which has relatively low fluid speed with fallen leaves. Except the case of mountain Inwang, other two collection points were typical and each pond looked temporary pond. Egg mass from Mountain Surak were collected at the small pond apart from the main stream and egg mass from Gwangju were collected from the small pond. Each egg mass which collected from three regions were kept in plastic container(29 long×16wide×19cm high), filled with 3l of dechlorinated tap water, separately with the supply of air at room temperature. The water temperature in the container ranged between 11 ~ 20°C throughout the experiment, and photoperiod was not controlled. The test was started the next day of the collection. Most eggs hatched approximately 2 weeks after the day of collection and during this two weeks, we remained each 27 egg mass in the each container with chemical cue treatment. After the hatching, we separated 8~10 larval salamanders from the egg mass and kept them in an independent container so that it could prevent larval salamanders from the

Table 1. Schedule of egg mass collecting

Date	No. of egg mass	Collecting location
2010. 03. 04	8	Mountain Inwang
2010. 03. 05	7	Mountain Surak
2010. 03. 26	6	Gwangju
2010. 04. 03	6	Mountain Inwang

Table 2. The number of larva according to conditions

	Group	Number of larvae	Number of groups
Pond	Predator cue treated	50	7
	No cue	37	4
Stream	Predator cue treated	27	3
	No cue	38	5

cannibalism and cannibal morph induction by high density (Table 2). In other words, if 24 larva hatched from one egg mass, two other test container would added according to the population, 8 individuals each.

2. Test Procedure

We made two groups of eggs for two different predation risks; predation cue injected and no predation risk circumstance. Predation cue injection was practiced thrice a day at 10:00, 13:00, and 16:00. Each treatment include 2ml of chemical cue following the well-established protocol (Brown *et al.*, 2006). When we treated the test animal, we injected the chemical cue along the container's wall not to disturb the test animals by the water waves. Chinese minnows were used as a predator indirectly by extracting their odor. Because Buskirk and Arioli (2002) found that predator odor itself is sufficient to initiate at least some components of the morphological defense of *R. lessonae* at metamorphosis and they responded to the number of dragonflies independent of the predator's diet. And in general, Chinese minnows are omnivorous which prey on aquatic plants, water beetles and small larval amphibians. In the stream environment, larval salamander could be predated by Chinese minnows. Thus we used them as a predator considering easy to collection. We captured three Chinese minnows from the pond in Mountain Bulam and fed them with commercial fish flake every other day. Predator cue was made everyday with 500ml dechlorinated tap water and one Chinese minnow by containing it for overnight following the preceded method so that the predator's odor can absorb to the water (Ferrari and Chivers, 2008; 2009b). Chemical cue source animal was changed everyday not to get the animals stressed. We conducted our test explained above from the next day of collection to the first one week after the hatching. After the test period ended, we measured all the

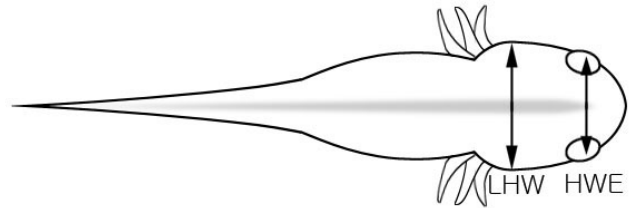
Figure 1. Dorsal projections of landmark locations on *H. ieechii* larvae reared in experiments

Table 3. Mean and SD values of svl and head size proportion

	Mean	SD
SVL	11.61	1.46656
Head size proportion	0.82	0.06630

salamander larvae's head size (Wakahara, 2001) and snout-vent length which used in test. First, we measured the head width at the level of the eyes (HWE) and the largest head width (LHW) (Figure 1). And we divide HWE by LHW of each individual larva to quantify the proportion of cannibal morph. Next, we also measured snout-vent length (SVL) to find out whether the correlation exists between predation risk level and body size. The mean and SD values of svl and head size proportion were tabulated below (Table 3).

3. Statistical analysis

To analyze data from the experiments that four groups of larvae, we used Mann-Whitney's test to determine significant changes in the proportion of head size and body size between each group. All tests were significant in alpha range 0.05 and all statistical analysis were performed using SPSS Ver. 18.0 (SPSS, Chicago, IL, U.S.A)

RESULTS

We compared the mean values of HWE/LHW and SVL of each group of larvae divided according to habitats using Mann-Whitney's. As a result, we found significant changes in HWE/LHW and SVL (Table 4). Larvae from stream showed increased head size proportion and SVL by the predator cue significantly. Larvae from pond also had significant change in SVL; however they showed non-

Table 4. The results of Mann-Whitney's test according to cue treatment and habitat

		Head size proportion	SVL
Cue treatment according to habitat	z	2.713	0.194
	p	< 0.05	> 0.05
No cue treatment according to habitat	z	4.391	3.555
	p	< 0.001	< 0.001

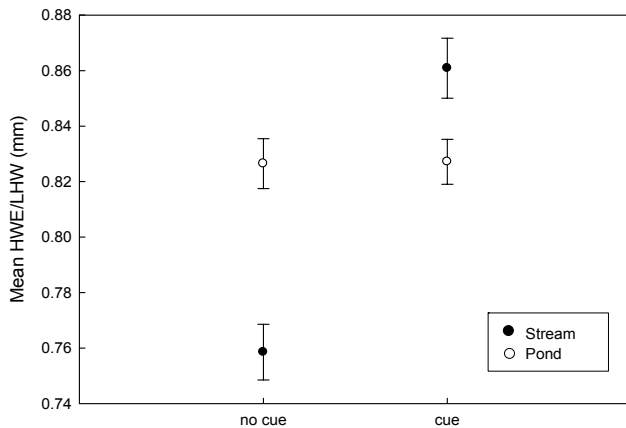


Figure 2. Larvae from stream showed significant changes in HWE/LHW, but larvae from pond had non-significant change in head

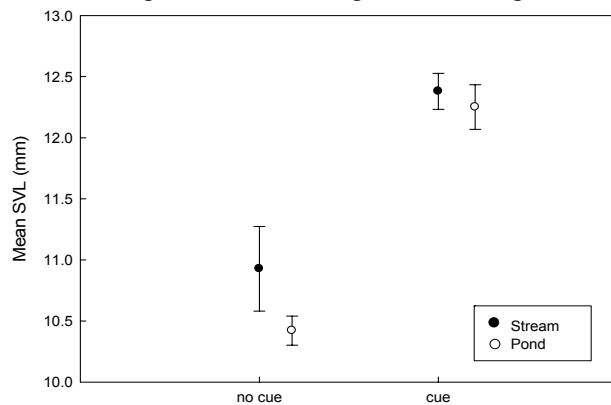


Figure 3. Larvae from stream and pond showed significant changes in SVL by the predator cue

significant changes in head size proportion by the chemical cue (Figure 2, 3).

DISCUSSION

In general, three reasons have been proposed to explain the induction of cannibal morphs: (1) to consume conspecifics because they provide a better balance of nutrients; (2) to

exclude potential competitors for food and/or space; and (3) to consume large, tough prey when other food resources are scarce (Michimae and Wakahara, 2002). However, our research suggests another reason for inducing cannibal morph in larval salamander. Our results indicate that cannibal morph of larval *H. ieechii* from stream environment was induced by the predation risk. This result is similar to the study which researched the predator-induced phenotypic plasticity in larval newts by Buskirk and Schmidt (2000). They showed that larval newt, Genus *Triturus* tended to induce broaden head morph in the environment with predatory dragonfly, though their broaden head was not for the cannibalism but for the prey which they can easily encounter from their refuge (Buskirk and Schmidt, 2000). In the case of salamander, cannibal morph of *H. retardatus* was induced by the presence of similar-sized heterospecific larvae in comparison to same density with conspecifics and it also induced by the higher density with mixed siblings (Michimae and Wakahara, 2002). And the head size proportion was significantly larger than pond environment in the cue treatment condition, however, larvae from pond environment showed any changes in head size by the predation risk. We suggest this reason was due to the different habitat circumstance. In the stream environment, Chinese minnows are the major predator to the larval salamander. However, in the pond habitat, Chinese minnows are not the major predator to them. So larvae from pond showed weak response to the Chinese minnow predator cue, and larvae from stream responded sensitively to the predation risk. Our result also means the larval salamander responded to the predator regardless whether it's major predator or not. Though larvae from pond can not encounter the Chinese minnow as a predator in the nature, they recognized and responded to their cue. This result is similar to the study which embryonic wood frogs learned to recognize the predators (Ferrari and Chivers, 2009a). And in the non chemical cue circumstance, we can see the average head size proportion of larvae from pond was larger than larvae from stream significantly. Organisms that use ephemeral habitats often show such a "fast" lifestyle; including shorter larval periods than those in more permanent habitats (Wilbur, 1980; 1984; Sih, 1987). Pond is an ephemeral habitats compared to stream. Therefore larvae which inhabit pond should be active searching for nutritious food to grow fast. And conspecific

larvae could be more nutritious than any other food resources, so consuming them; they could grow faster and reach metamorphosis sooner than others (Wakahara, 1997). We suppose this would be the reason why the head size proportion of larvae from pond is larger than larvae from stream.

We also found out significant snout-vent length changes by the predator cue in larvae from both habitats. Under the constant risk treatment, large body size of tadpole, *R. temporaria* indicates that increased investment in defenses entailed a delayed metamorphosis at a larger size (Laurila *et al.*, 2004). Also, there was a report that larger larvae tended to be more exposed than smaller larvae in both the presence and absence of fish chemical cue, and showed stronger responses to chemical cues than did smaller larvae. These results provide mixed support for the a priori prediction that larger larvae should hide more effectively from fish than smaller larvae (Sih *et al.*, 2002). And there was a research which proved morphological change by the number of the predators and prey consumption levels (Buskirk and Ariol, 2002) just like our research. From these points of view, enlarged SVL of larval Korean salamander at one week after the hatching by the predation risk could be one of the survival tactics for them to avoid the predation risk effectively.

ACKNOWLEDGEMENT

Thanks to Eol and Eunji who drew me a lovely figure of salamander, and thanks Jonghyun, Miae and Dambi, too.

LITERATURE CITED

- Altwegg, R. and H.U. Reyer(2003) Patterns of natural selections and evolution of species. *Science* 294: 321-326
- Berven, K.A.(1990) Factors affection population fluctuations in larval and adult stages of the wood frog(*Rana sylvatica*). *Ethology* 71: 1,599-1,608.
- Brown, G.E., A.C. Rive and M.C.O. Ferrari(2006) The dynamic nature of antipredator behavior: prey fish integrate threat-sensitive antipredator responses within background levels of predation risk. *Behav. Ecol. Sociobiol.* 61: 9-16.
- Buskirk, V.J. and B.R. Schmidt(2000) Predator-induced phenotypic plasticity in larval newts: trade-offs, selection, and variation in nature. *Ecology* 81: 3,009-3,028.
- Buskirk, V.J. and M. Arioloi(2002) Dosage response of an induced defense: How sensitive are tadpoles to predation risk?. *Ecology*, 83 (6): 1,580-1,585.
- Buskirk, V.J., C. Muller, A. Portmann and M. Surbeck(2002) A test of the risk allocation hypothesis: tadpole responses to temporal change in predation risk. *Behav. Ecol.* 13(4): 526-530.
- Clark, C.W.(1994) Antipredator behaviour and the asset protection principle. *Behav. Ecol.* 5: 159-170.
- Crump, M.L.(1990) Possible enhancement of growth in tadpoles through cannibalism. *Copeia*, pp. 560-564.
- Crump, M.L.(1992) Cannibalism in amphibians. in Elgar MA, Crespi BJ, eds. *Cannibalism: ecology and evolution among diverse taxa*. Oxford, Oxford University Press, pp. 256-276.
- Elgar, M.A. and B.S. Crespi(1992) Cannibalism in amphibians. in Elgar MA, Crespi BJ, eds. *Cannibalism: ecology and evolution among diverse taxa*. Oxford, Oxford University Press, pp. 256-276.
- Ferrari, M.C.O. and D.P. Chivers(2008) Cultural learning of predators in mixed species assemblages: the effects of tutor-to-observer ratio. *Anim Behav.* 75: 1,921-1,925.
- Ferrari, M.C.O. and D.P. Chivers(2009a) Sophisticated early life lessons: threat-sensitive generalization of predator recognition by embryonic amphibians. *Behav. Ecol.* 20: 1,295-1,298.
- Ferrari, M.C.O. and D.P. Chivers(2009b) Temporal variability, threat-sensitivity and conflicting information about the nature of risk: understanding the dynamics of tadpole antipredator behaviour. *Anim. Behav.* 78: 11-16.
- Houston, A.I., J. McNamara and J.M.C. Huthcinson(1993) General results concerning the trade-off between gaining energy and avoiding predation. *Philos. Trans. R. Soc. Lond. B.* 341: 375-397.
- Jackson, M.E. and R.D. Semlitsch(1993) Paedomorphosis in the salamander *Ambystoma talpoideum*: effects of a fish predator. *Ecology* 74: 342-250,
- Josh, Van Buskirk and B.R. Schmidt(2000) Predator-induced phenotypic plasticity in larval newts: trade-offs, selection, and variation in nature. *Ecology* 81(11): 3,009-3,028.
- Kats, K.B. and K.M. Dill(1998) The scent of death : chemosensory assessment of predation risk by prey animals. *Ecoscience* 5: 361-394.
- Laurila, A., Jarvi- Laturi, M., Pakkasmaa, S. and Merila, J. (2004) Temporal variation in predation risk : stage-dependency, graded responses and fitness costs in tadpole antipredator defenses. – *Oikos* 107:90-99
- Mcpeck, M.A.(1990a) Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology* 71: 83-98.
- Mcpeck, M.A.(1990b) Behavioral differences between *Enallagma*

- species(Odonata) influencing differential vulnerability to predators. *Ecology* 71: 1,714-1,726.
- Merilia, J. and P. Crnokrak(2001) Comparison of marker gene and quantitative genetic differentiation among populations. *J. Evol. Biol.* 14: 892-903.
- Michimae, M. and M. Wakahara(2001) Factors which affect the occurrence of cannibalism and the broad-headed "cannibal" morph in larvae of the salamander *Hynobius retardatus*. *Behav. Ecol. Sociobiol.* 50: 339-345.
- Michimae, M. and M. Wakahara(2002) A tadpole-induced polyphenism in the salamander *Hynobius retardatus*. *Evolution* 56(10): 2,029-2,038.
- Park, S.R., J.Y. Jeong and D.S. Park(2005) Integrative. *Biosciences* 9: 13-18.
- Pfenning, D.W.(1997) Kinship and cannibalism. *Bioscience*, vol. 47, No. 10, AIBS: The First 50 Years. Nov., pp. 667-675.
- Polis, G.A.(1981) The evolution and dynamics of intraspecific predation. *Anny. Rev. Ecol. Syst.* 12: 225-251.
- Richardson, J.M.L.(2001) A comparative study of activity levels in larval anurans and response to the presence of different predators. *Behav. Ecol.* 12(1): 51-58.
- Schlichting, C.D. and M. Pigliucci(1998) Phenotypic evolution: a reaction norm perspective. Sinauer Associates, Sunderland, Massachusetts, USA.
- Scott, D.E.(1994) The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology* 75: 1,383-1,396.
- Sih, A., R. Ziemba and K.C. Harding(2000) New insights on how temporal variation in predation risk shapes prey behaviour. *Trends. Ecol. Evol.* 15: 3-4.
- Sih, A.(1987) Predators and prey life cycles: an evolutionary and ecological overview. - In: Kerfoot, W. C. and Sih, A.(eds), *Predation: direct and indirect impacts on aquatic communities*. Univ. Press of England, Hanover, NH, pp. 203-244.
- Sih, A., B.K. Lee and E.F. Maurer(2002) Behavioral correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. *Anim. Behav.* 65: 29-44.
- Skelly, D.K.(1997) Tadpole communities. *Am Sci* 85: 36-45.
- Smith, D.C.(1987) Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology* 68: 344-350.
- Stemberger, S.S. and J.J. Gilbert(1987) Multiple-species induction of morphological defenses in the rotifer *Keratella testudo*. *Ecology* 68: 370-378.
- Tollrian, R. and C.D. Harvell(1999) The ecology and evolution of inducible defenses. Princeton Univ. Press, Princeton, New Jersey, USA.
- Turner, A.M., R.J. Bernot and C.M. Boss(2000) Chemical cues modify species interactions; the ecological consequences of predator avoidance by freshwater sails. *Oikos* 88: 148-158.
- Wakahara, M.(1997) Kin recognition among intact and blinded, mixed-sibling larvae of a cannibalistic salamander *Hynobius retardatus*. *Zool. Sci.* 14: 893-899.
- Wakahara, M.(1995) Cannibalism and the resulting dimorphism in larvae of a salamander *Hynobius retardatus*, Inhabited in Hokkaido, Japan. *Zoological science* 12: 467-473.
- Wellborn, G.A., D.K. Skelly and E.E. Werner(1996) Mechanism creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.* 27: 337-363.
- West-Eberhard, M.J.(1989) Phenotypic plasticity and the origins of diversity. *Annual Reviews* 20: 249-78.
- West-Eberhard, M.J.(1992) Behavior and evolution. In *Molds, molecules and metazoan: growing points in evolutionary biology* (ed. Grant, P.R. and H.S. Horn), pp. 57-75. Princeton University Press.
- Wilbur, H.M.(1980) Complex life cycles. *Annu. Rev. Ecol. Syst.* 11: 67-93.
- Wilbur, H.M.(1984) Complex life cycles and community organization in amphibians. - In: Price, P.W., C.N. Slobodchikoff and W.S. Gaud(eds), *A new ecology: novel approaches to interactive systems*. Wiley. New York, pp. 195-226.
- Wiseden, B.D.(2000) Olfactory assessment of predation risk in the aquatic environment. *Phil. Trans. R. Soc. Lond. B.* 355: 1,205-1,208.
- Yang, S.Y.(2001) Monograph of Korean Amphibia. Academy books, Seoul, Korea, 55pp. (in Korean)