Korean J. Zool. 39:437-446, 1996

Courtship, Fighting Behaviors and Sexual Dimorphism of the Salamander, *Hynobius leechii*

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The courtship and fighting behaviors and the sexual dimorphism of the salamander *Hynobius leechii* were studied. The parameters, snout vent length, body length (from snout to tail tip), and proportion of snout vent length to body size were larger in the female than the male. Five physical parameters in males were significantly correlated with one another, body length, snout vent length, head width, tail vent length, and tail depth, while all, except tail depth, were significantly correlated in females. Sexual behavior of *H. leechii* involved external fertilization and consisted of three stages, identifying the female, attracting the female, and insemination. The identification stage consisted of a positive advance by the male toward the female and display of snout contact. The male attracted the female with chin rubbing, tail undulation, smelling, and digging displays. The insemination process consisted of four phases, amplex, separating egg sacs from the female's cloacal, fertilizing eggs, and post fertilization. Fighting behaviors were quite simple. The attacking male would generally bite the opposite male's upper chin or hind limbs and then shakes his head two or three times. The bitten male, which in most cases was of a dissimilar body size, quickly escaped from the attacking male. After fighting, winning male usually displayed rapid tail undulation.

KEY WORDS: *Hynobius leechii*, Courtship Display, Sexual Dimorphism, Fighting Behavior

The full understanding of a biological system requires parallel consideration of both the form and the function of that system. This basic approach, the essence of post-Darwinian biology, has been widely applied to the morphology and physiology of animals and, in recent years, to some aspects of their behavior (Baerends *et al.*, 1976).

In most salamanders (about 90% of all species), fertilization is internal; the male deposits sperm packets (spermatophores) on the substratum, which the female takes into her vent (Stebbins and Coher, 1995). External fertilization occurs in only two families of salamanders, the Hynobiidae and the Cryptobranchidae, and takes place in water during mating (Salthe, 1967; Arnold, 1977).

In *H. retardatus*, sexual behavior begins with the female attaching her egg sacs to an object and several males subsequently approaching and pushing her away from the sacs. At the same time they rub their cloacal over the sacs and ejaculate milt (Thorn, 1962). During this process, two or more males may show aggression towards one another. This aggression is apparently directed towards the defence of egg sacs rather than defence of the female, and probably serves as a form of paternity assurance (Salthe, 1967; Halliday and Verrell, 1984). In Crytobranchus the

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male follows a female with protruding egg strings beneath a rock, and fertilizes them as they are extruded (Smith, 1907). There is no known courtship ritual in these genera, but because the eggs are laid in sites chosen by the male, there may be a form of behavior directing the female into his territory (Thorn, 1963; Slathe, 1967).

Hynobius is a genus of the family Hynobiidae. It is confined to the eastern Asiatic region and is the most primitive group of urodeles (Kusano, 1980). Three species of Hynobius are found in Korea. *H. leechii* is distributed in the all regions of the Korean peninsula below latitude 40° including jeju island. Like other salamanders, this species is a small poikilotherm which leads a terrestrial life in the non-breeding season and returns to the water to breed in early spring. It has an aquatic larva and breeds in flowing water in hilly regions.

Although some intensive studies have been performed with certain North American plethodntid salamanders (Tilley, 1973; Verrell, 1991) and a European salamandrid newt (Halliday, 1974; Raxworthy, 1989), there are no satisfactory behavioral studies of salamanders in Korea. In this study, we carried out morphological and behavioral studies of *H. leechii*, chiefly on the courtship, insemination, and fighting behaviors.

Materials and methods

H. leechii in full breeding condition were collected Choongju, Chungju in Chungbuk, and Hamyang in Kyeongnam. Nineteen individuals were collected in 1995 and 89 in 1996. Males and females were kept in separate aquaria (1200 $\times 300 \times 400$ mm) containing gravel and planted pond weed at a temperature of approximately 9-15°C. Mealworm and freshwater amphipod, Gammarus were provided as live foods. The light schedule was set to match the local (36° latitude) photoperiod.

To analyze sexual dimorphism, 88 of the 108 individuals, 70 males and 18 females were used. Body length, snout vent length, tail vent length, weight, and tail depth were measured using a vernier caliper. For statistical analyses, one-way ANOVA, kruskal-walis test, correlation, and discrimination analyses were used.

Courtship and fighting observations were made between 18:30 and 22:00 hours in aquaria of dimensions $450 \times 300 \times 300$ mm containing sand. The observation tanks were kept at the same temperature as the stock tanks. A total of 34 males and 18 females was used. Courtship trials were performed with pairs of salamanders or two males and one female, and the males were introduced into the tanks 30 minutes prior to the females. For fighting trials, two or three males were used with one female. In this case, females were placed into the observation tank 20 minutes prior to the males.

A one hour spoken commentary was recorded for all trials using a tape recorder beginning 30 minutes after the above stated treatments. The recording was timed and transcribed. A colour video recorder was also used to film several courtship trials including 3 in which insemination took place.

Results

Sexual dimorphism

Females were found to be significantly larger than males in the sample of 88 individuals studied. The mean snout vent length was 61.6 mm for males (SD 4.5. range 51.0~75.0, n=70) and 66.5 mm for females (SD 5.9, range 52.9~72.5, n=18) ($F=14.82$, $df=1$, $P<0.001$). The mean body length for males was 113.1 mm (SD 8.8, range 96.0~134.5, n=70) and for females was 117.9 mm (SD 10.1, range 94.0~136.4, n=18) ($F=4.23$, $df=1$, $P<0.05$). The snout vent length to body length ratio was significantly higher in females (1:0.56, n=18) than in males (1:0.54, n=70) ($F=15.91$, $df=1$, $P<0.001$). The mean head width (1.16 ± 0.09, n=88) and tail depth (0.74 ± 0.09, n=88) were not significantly different between males and females.

Correlation between males and females in parameters of body size, snout vent length, head width, weight, tail vent length, and body length were analyzed (Table 1). In males, all parameters were significantly correlated with each other ($P<0.001$) while, in females, all parameters but tail

depth were significantly correlated ($P<0.001$). The percentage of grouped cases, which were correctly classified from the results of discriminant analysis using five parameters, was 88.64% (Table 2).

Courtship and insemination

Male courtship behaviour consists of the two stages, identifying and attracting the female. The former comprises two displays, the advance towards the female, and making snout contact with her. The latter stage comprises the chin rubbing, smelling, tail undulation, and digging displays (Fig. 1, Table 3).

Contact between the male and female is initiated by a direct approach from the male. A sudden movement by the female typically first draws the male's attention so that he turns towards her. The male first turns his neck towards the female and approaches with a head down posture, advances towards the female display. The male usually repeats the approaching and pausing movements about 3~5 times until he makes contact with the female's snout.

After a period of snout contact between the male and female (Fig. 2), the male initiates his tail undulation display which then continues for all courtship stages except insemination. The male also commences the chin rubbing, smelling, and digging displays. Female to male's chin rubbing, rubbing his chin against female's head, pauses without movement or turns her head from the male's display. Smelling behavior, involving contact of the male's snout against the female's body, is long-lasting. When the male first makes contact with the female's head, smelling progresses from female's head or vent to her cloacal. If the first contact is with female's tail, smelling progresses from the cloacal or vent to the head.

The male also continuously conducts a digging display, advancing beneath the female's body using his head and fore limbs against the fore limbs, vent, and cloacal of the female. After successive digging actions, the resulting posture is that male's head or vent is placed beneath the female's body, and the male becomes still beneath the female's body, while his tail undulation becomes faster. At this point male almost sees the female's head or eyes. If the female avoids the male's attracting displays, the male slowly pursues

Table 1. The correlation among dimorphic charateristics of 70 males and 18 females

Sex	Males				Females			
Parameters	Snout Vent Length	Head Width	Weight	Tail Vent Length	Snout Vent Length	Head Width	Weight	Tail Vent Length
Head Width	0.7581**				0.7662**			
Weight	0.7897**	0.8460**			0.8925**	0.7957**		
Tail Vent Length	0.7082**	0.7044**	0.7604**		0.6876**	0.7658**	0.8066**	
Tail depth	0.5356**	0.6566*	0.7833**	0.6664**	0.1122	0.1443	0.3917	0.4077

**; $P < 0.001$

Table 2. Discriminant analysis between males and females by the five dimorphic charateristics of 88 individuals

Actual Group	No. of Cases	Predicted Group Membership	
		Male	Female
Male	70	63	7
		90.0%	10.0%
Female	18	3	15
		16.7%	83.3%

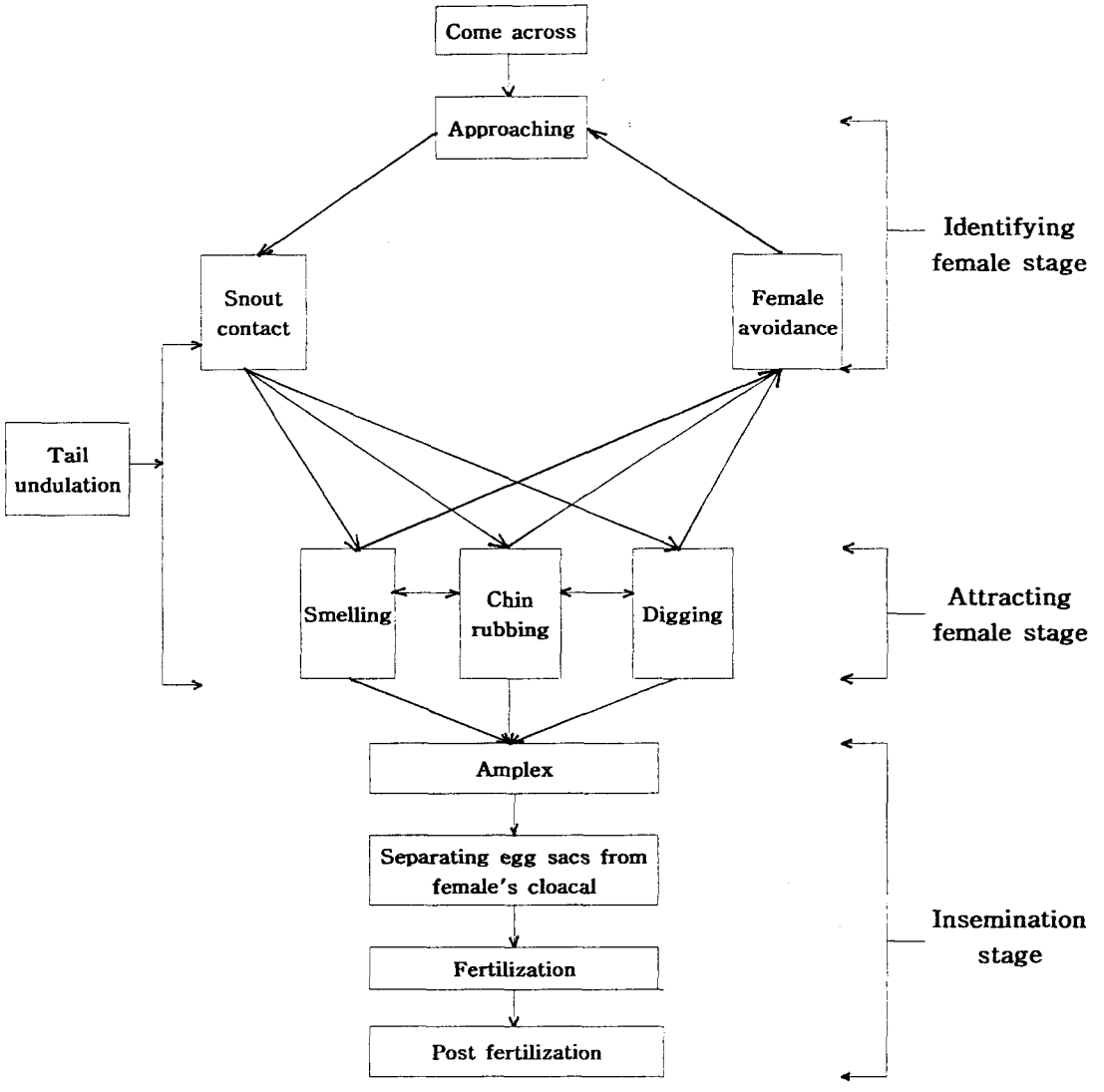

Fig. 1. The sexual behavior sequence of the *Hynobius leechii*'s male. The sexual behavior consists of the identifying female, attracting female and insemination stages.

the avoiding female with a head down posture to within about 10 cm of the female. Although there is a variation in tail undulation frequency during this process, tail undulation is continuous.

When the male take-up the female, the female continuously tries to avoid the male or turns her neck towards other approaching males and moves towards them. During the smelling display, which begins after approaching the avoiding female, the frequency of the male's tail undulation generally increases and width range of his tail undulation becomes widely extend. If the female avoids the male's display again, the male continues tail undulation only and waits until she is about 10 cm away from him. If the female is too far away from the male, more than about 10 cm, the male pursues her again in two ways, one following her tail movement, the other directly approaching her head or body. After a successful pursuit, the male again conducts smelling, digging and ching

Table 3. Dispaly names, definition, and description used in this study of *Hynobius leechii's* courtship

Display name		Definition	Description	Names used by earlier atuthors
Tail undulation		The male's tail is held out directly behind his body and vibrates slowly or quickly so that waves pass down to the tip of the tail.	This display is used continuously during all courtship stages except insemination. It is thought to transport pheromones to the female.	Raxworthy (1989)
Positive advance	Head down posture	Male movement towards the female with his head down; seen in earlier stage of courtship.	This movement is repeated as a slow and fast movement and the male places his snout against the female's snout using a fast movement when 3~4 cm apart.	Uzendoski & Verrell (1993, review)
	Head and front limbs up posture	Male mevement tawards the female with his fore limbs and head up as if jumping; seen in middle stage of courtship.	Turning behavior about 180° coincides with this behavior so that the male can move about 5~7cm towards the female. It is also seen during the post fertilization stage.	none
Snout contact		Male's snout contacts with female's snout.	This display is conducted in two parts. Firstly, two opposed individuals move towards each other, then, when one individual approaches the other to within about 2-3cm, the other individual quickly turns his/her head to the approaching individual. This is a method to identify the female.	none
Chin rubbing		Male rubs his chin against female's head.	The male puts his chin (down ro up) on or beneath the female's head. This display is thought to induce female control or attraction.	Uzendoski & Verrell (1993, review)
Digging		Male advances beneath the male's body using his head and fore limbs.	After successful digging, the male remains beneath the female's body with fast undulation. This display is considered to be a process that attracts the female and stimulates the female's production of egg sacs.	none
Smelling		Male makes contact with the female's skin with his snout.	If the male first contacts the female's head, smelling progresses from the female's head, to vent to cloacal, while if the first contact is with the female's tail, smelling progresses from cloacal to vent and head. It is considered to be a process by which the male assesses the female's fecundity.	Uzendoski & Verrell (1993, review)

rubbing displays. Although less frequent, some females also conduct smelling, digging, and chin rubbing displays against the displaying male.

At courtship display of 28 times, measured over a period of 60 minutes, all displays among individuals were significantly different (one-way ANOVA: $P<0.01$ to number of tail undulation, kruskal-walis test: $P<0.01$ to others parameters, Table 4). Tail undulation was induced by seeing the female and by positive advances towards the female and, after initiation of tail undulation, smelling displays were continuously conducted ($r=0.4342$ and 0.6812 respectively, both $P<0.001$). The female's avoidance of the male's displays, except for tail undulation, was a general pattern ($P<0.001$, Table 5).

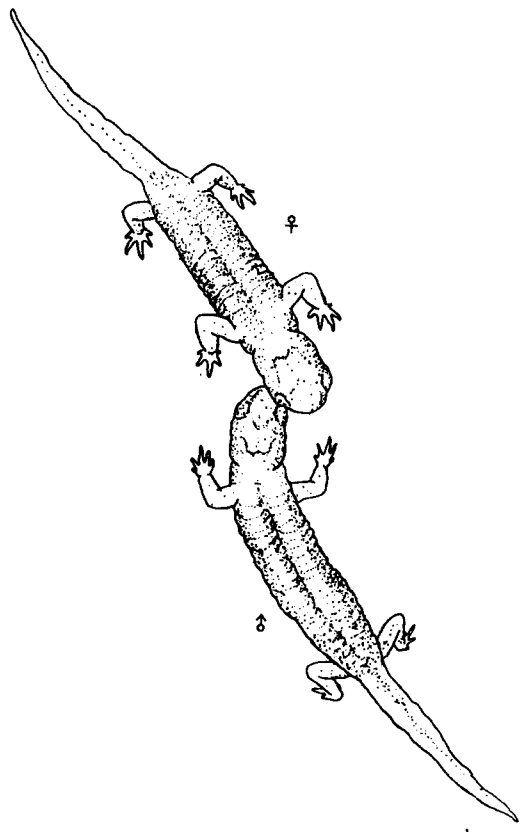

Fig. 2. The snout contact display of the *Hynobius leechii* in the identifying female stage. This display is a method to identify the female.

Insemination consists of amplex, extruding egg sacs, fertilization, and post fertilization phases. Insemination is initiated by the male catching the female's dorsal gland with his fore limbs (Fig. 3). At this point, if the egg mass protrudes from the female's cloacal, the male's head turns directly towards the female's cloacal and he grasps the female with his hind limbs again, thus freeing his fore limbs. If the egg mass is not protruding, the male uses his hind limbs to extrude the egg mass from her cloacal. To do this, the male catches the female's hind dorsal gland with his fore limbs and extrudes the egg mass with his hind limbs, expressing them from the vent of the female's body.

When the egg mass is slightly extruded from her cloacal, the male catches the egg sac with his fore limbs and mouth. In this stage, the female's movement is dependent on the male's behavior such that the male and female cross over each other about two or three times. While catching the egg sacs with his mouth and fore limbs, the male moves his hind limbs in order to place the egg sac between his hind limbs and tail. At the same time, the male's hind limbs push the female's body (Fig. 4). The egg sacs are therefore separated from the female's cloacal. The mean time taken from catching the female's vent to separating the egg sacs from the female is 21 ± 1.3 sec (n=3).

To release sperm onto the egg mass, the male wraps his body around the egg sacs which are held between his fore limbs, mouth and hind limbs. He

Table 4. The charateristics of *Hynobius leechii*'s courtship behaviors. These data were collected from 28 sucessful trials

	No. of Tail Undulation	No. of Seeing and Advance	No. of Smelling	No. of Snout Contact	No. of Female's Avoiadance
Mean±SD (Min~Max.)	307.39±164.11 (89~721)	10.89±6.19 (1~27)	7.29±3.83 (0~17)	1.68±1.59 (0~7)	3.82±3.92 (0~15)

Table 5. The correlation among *Hynobius leechii*'s courtship behaviors

	Tail Undulation	Seeing and Advance	Smelling	Snout Contact
Seeing and Advance	0.4342**			
Smelling	0.1920	0.6812**		
Snout Contact	0.1108	0.2488	0.3020	
Female's Avoidance	0.2389	0.6729**	0.6384**	0.4668**

**; $P < 0.001$

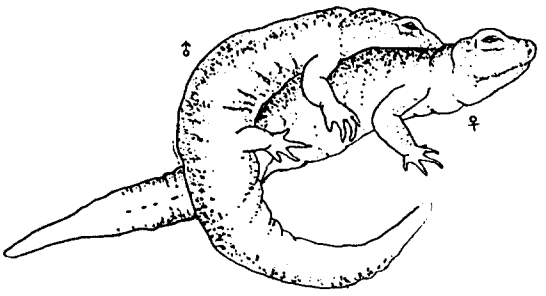

Fig. 3. The amplex of the *Hynobius leechii* in the insemination stage.

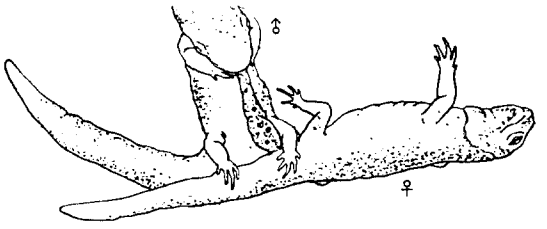

Fig. 4. The extruding egg sacs from the female's cloacal in the insemination stage. In order to separate the egg sacs, male generally uses his hind limbs and mouth.

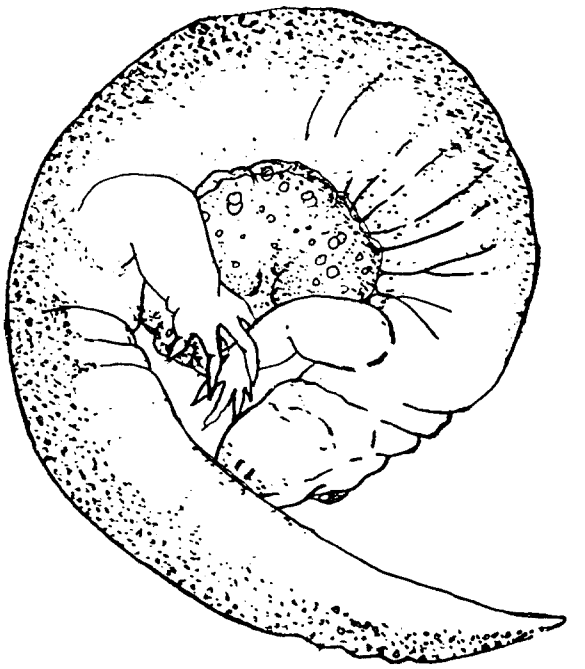

Fig. 5. The fertilization display of *Hynobius leechii*. In order to release sperm onto the egg mass, the male wraps his body around the egg sacs which are held between his fore limbs, mouth and hind limbs. He then scratches the egg sacs with his hind limbs.

then scratches the egg sacs with his hind limbs (Fig. 5). This fertilization takes approximately 27 ± 12.8 (n=3) sec. After fertilization, the male remains in a wrapped-around position for a short period. One of the individuals tested kept his mouth fully open during this period. Approximately 182.6 ± 13.4 sec (N=3) after catching the female's dorsal gland, the male releases the egg mass from his body. The male then assumes the head and fore limb up posture and undulates his tail, the vibration progressing quickly from the base to the tip of the tail in a zigzag curve, this occurring within 10 cm of the eggs. During the post fertilization display, if the male again finds the egg sac which he has fertilized, he again wraps his body around the fertilized sacs, and this may be repeated this two or three times.

Fighting behaviour

In most cases, a direct encounter between two males initiates fighting behavior. When two males make snout contact, if one male avoids the other's head, then no fight occurs. Otherwise one male generally bites the other on the upper chin while performing quick zigzag tail undulations wavering from the first third of the tail to its tip. The biting male shakes his neck about two or three times and then releases the bitten male. In most cases the bitten male quickly runs away. The winning male shakes his body back and forward at the fighting site and moves around with his tail undulating quickly. If the same two males meet again, the defeated male usually runs away after snout contact. In our observations, there was no apparent correlation between body length and the proportion of wins. In general, the male who attacks first wins.

Discussion

Our finding, that the female salamander is larger than the male in snout vent and total body length, supports that body length sexual dimorphism in urodeles is generally slight or absent. Moreover, the significance of body length differences between the sexes lies not in male fighting behavior, but in the relationship of male and female fecundity (Halliday and Verrell, 1986a). The finding, that the ratio of snout vent length to total body length is larger in the male than the female, also supports this conclusion. In the male, tail depth was correlated with the other parameters of body size, while no such correlation was observed in the female. This suggests that tail depth is the only parameter which is related to courtship behavior in that the tail is frequently used for achieving undulation and positive advance displays.

The male's repetition of slow and quick movements close to the female has been proposed as the means of visually claiming the female since, in case of other approaching males, such movement cannot be seen (Stebbins and Coher, 1995). In general, after snout contact display, the male decides the next display, uninteresting in the case of male or interesting in the case of female. This result indicates that snout contact is also a process of claiming the female by touch and smell. Pheromones are released from the skin and cloacal and these clearly play an important role in salamander sex recognition (Sever, 1988a; Houck and Reagan, 1990). The tail undulation of *H. leechii* was initiated from cloacal the cloacal region where most salamanders have the dorsal gland (Sever, 1988b). This finding suggests that our species may also produce courtship pheromones during the tail undulation display and that a cloacal pheromone may play a role in identifying and attracting the female. In many salamanders, the males touch the female's skin with their snouts (Arnold, 1977). The female salamander possesses a highly vascular and permeable skin and it is through this that the olfactory cue (vitellogenin) to her fecundity is available for the male to assess (Stebbins and Coher, 1995). A smelling display may also be considered an affirmation of the female's fecundity. After pairings occurs in salamander, a variety of methods are used to induce female reception and control (Marvin and Hutchison, 1996; Houck and Reagan, 1990). The chin rubbing display of *H. leechii* was also though to be a process to induce female control or attraction since the male courtship glands commonly occur on the chin, on the side of the head, or upper base of the tail (Sever, 1989). The function of digging is not clear. However, it may also have a stimulus action on female reception since if digging were successful, the male's tail undulation increases and his vision is almost fixed to the female's head or eye. The digging display might also be considered a stimulus for extruding egg sacs because, during the male's tail undulation under the female's body, the female's body is vigorously shaken.

From the correlation analyses of the displays, tail undulation generally follows the seeing and positive advance behaviors after which smelling was initiated. Most of the female's avoidance of the male occurs after seeing and advance, smelling, and snout contact. Sometimes when the male displays smelling, the female responds to the male with seeing, approaching, and then smelling.

At this point the male moves or remains still to the female's responses. This results suggest that displays of smelling, chin rubbing, and digging may commonly play a role in the attraction and persuasion of the female. In the attraction and persuasion process, pheromones may also be used.

To date, there has been little detailed study of the external fertilization process of salamanders. When the female attaches the ends of her egg sacs to an object or extrudes egg sacs from her cloacal, the male follows and fertilizes them (Smith, 1907). Although our individual did not perfectly extrude her egg sacs from her cloacal, the male fertilized the eggs after himself extruding the egg sacs by using his hind limbs to express them from her vent. In this situation, the female and male are joined and rotate together 3-5 times. After extruding her egg sacs, the female displays seeing, approaching, and smelling behaviors to the male, rather than attacking him. During fertilization, the male usually uses his hind limbs to cover the egg sacs with his sperm and his perfectly round posture keeping the egg sacs inside his vent, is known as a paternity process (Halliday and Verrell, 1984). The function of the post fertilization display is not clear, but we believe it may be related to protection of eggs and to affirmation of the male's paternity. Our studies, and those of Kusano (1980), indicated that most males remain near the egg sacs after fertilization.

Fighting behaviour appears to be rare in urodeles (Halliday and Verrell, 1986b) and *T. vittatus* is probably unique among the Triturus newts in that aquatic males are intolerant to each other, to such an extent that they may fight to the death if confined together (Lantz, 1912). Our specie usually bites the opposite male and, after shacking him two or three times, releases the bitten male without further attacks. That male's shows of strong tail movements after fighting may be considered a display of his win, but its function is not clear still. Our finding, stated above, that the win rate was not related to body length also indicated that the body length of our species implies sexual fecundity.

In conclusion, sexual behaviour employing internal fertilization comprises identifying a receptive female, courtship behavior, depositing the spermatosphore, and picking up the spermatosphore (Salthe, 1967; Halliday, 1974), while the behavior of *H. leechii* generally consists of identifying the female, attracting her, and insemination. The tail undulation and smelling displays of *H. leechii* suggest that our species may use pheromones in courtship. Since these results were obtained in a laboratory situation, the field studies are still necessary to obtain further information on the evolutionary function and mating system of this Korean salamander.

Acknowledgements

This study was supported by the Basic Research Institute Program (BSRI-95-4423), Ministry of Education, Korea. We especially thank Byunggun Lee, Ouedong Han, Sukhwan Jung for their helpful field and laboratory works.

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(Accepted October 12, 1996)

한국산 도롱뇽의 구애행동, 싸움행동 및 신체적 특징

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한국산 도롱뇽(*Hynobius leechii*)의 암수의 신체적 특성 및 구애, 싸움 행동에 대한 연구를 수행하였다. 몸의 길이, 코부터 총배설강까지의 길이, 몸의 길이에 대한 코부터 총배설강까지 길이의 비에 있어서 암컷이 수컷보다 더 길었으며, 수컷들은 몸의 길이, 코부터 총배설강까지의 길이, 머리의 넓이, 꼬리부터 총배설강까지의 길이, 꼬리의 넓이의 5개 요소에 있어서 모든 요소들이 서로 유의미한 상관을 보인 반면, 암컷에 있어서는 꼬리의 넓이를 제외한 모든 요소에서 의미 있는 상관을 보였다. 체외수정을 하는 한국산 도롱뇽의 성적인 행동은 암컷을 확인하는 단계, 암컷을 유인하는 단계, 그리고 수정 단계로 구성되어진다. 암컷을 확인하는 단계는 암컷에게로 접근 행동 및 서로 코를 맞대는 행동으로 구성되며, 유인 단계에서는 턱부비기, 꼬리치기, 냄새맡기, 파기의 네 가지의 과시 행동이 나타났다. 수정의 과정은 포접, 암컷으로부터 알주머니의 분리, 알의 수정, 수정 후 과시 행동으로 구성되었다. 싸움 행동은 간단한 편으로, 공격하는 개체는 상대편의 위턱이나 뒷다리 부근을 주로 물었으며, 문 상태에서 자신의 머리를 2-3회 흔드는 행동을 보였다. 대부분의 경우에 있어서 개체의 크기에 상관없이 공격을 당한 개체는 공격한 개체로부터 재빨리 회피를 하였으며, 승리를 한 개체는 빠른 꼬리치기 과시 행동을 보였다.