

Effects of Physical Parameters and Age on the Order of Entrance of *Hynobius leechii* to a Breeding Pond

Lee, Jung-Hyun and Daesik Park*

Division of Science Education, Kangwon National University, Chuncheon, Kangwon 200-701, Korea

ABSTRACT: To determine the age structure of a *Hynobius leechii* breeding population and analyze relationships between the order of entrance to breeding ponds and physical parameters and age, we studied a wild population of the species in the Research Forests of Kangwon National University in Chuncheon, Kangwon, South Korea from March 16 to April 13, 2005. The age of breeding males ranged one to nine years old and that of females ranged from three to nine years old. The asymptotic sizes of males and females were 6.36 and 6.51 cm, respectively, and the growth coefficients of males and females were 0.71 and 0.81, respectively. The snout-vent length (SVL), head length, and body mass of males were all positively correlated with their age, but female age did not show a significant relationship with any physical parameter. The tail depth, body mass, and condition factors (SVL/body mass \times 100) of both males and females were negatively related with the order of entrance to the breeding pond. The head width and SVL of males were also negatively correlated with the order of entrance, but the SVL of females was positively related with the order of entrance. These results suggest that physical parameters are more important determinants of breeding migration patterns than age. We discuss which of two hypotheses, the mate opportunity hypothesis and the susceptibility hypothesis, is better able to explain the order of entrance to breeding ponds for male and female *H. leechii*.

Key words: Amphibian, *Hynobius leechii*, Mate opportunity hypothesis, Migration, Salamander, Skeletochronology, Susceptibility hypothesis

INTRODUCTION

In many different animal taxa inhabiting temperate zones, breeding males arrive at breeding sites earlier than breeding females (Morbey and Ydenberg 2001), a pattern referred to as protandry. Several different hypotheses, such as rank advantage (Ketterson and Nolan 1976), mate opportunity (Iwasa et al. 1983, Douglas 1979, Semlitsch et al. 1993, Lodé et al. 2005), mate choice (Wang et al. 1990), constraint (Gauthreaux 1978, Wiklund and Solbreck 1982), and susceptibility (Ketterson and Nolan 1983), have been proposed to explain protandry. In amphibians, the mate opportunity hypothesis-that breeding males arrive at a breeding site earlier than females to increase their mating opportunities-has been widely accepted as the most plausible hypothesis, but has not been directly investigated. However, a recent study (Miwa 2007) showed that the time of amphibians' breeding migrations is affected by environmental conditions in their hibernation sites in early spring, which is more compatible with the susceptibility hypothesis.

The operational sex ratio (OSR) of *Hynobius leechii* in breeding populations was male-biased, with about 1 female for every 3.8 males (Park and Park 2000), so males are faced with strong intra-

sexual competition for mating opportunities. In general, three to four males simultaneously mate with a single female (Park et al. 1996, Park and Park 2000). Breeding males arrive at a breeding pond two to three days earlier than females and stay at the pond for approximately 10 days (Sung et al. 2005). During the breeding season, since few food resources are available in breeding ponds, males staying at the ponds lose substantial proportions of their body mass, but these males may also participate in multiple matings, potentially resulting in increased reproductive success. Females generally arrive at breeding ponds when it is raining (Sung et al. 2005). During a breeding season, therefore, the OSR varied greatly depending on how many males stayed in a pond and how many females arrived at the pond on a specific day (Park and Park 2000, Sung et al. 2005). Although previous studies have reported that breeding males arrive earlier than females at breeding ponds, they have not explored how different physical parameters and individual age affect the order of entrance of *H. leechii* to breeding ponds.

If the order of entrance of *H. leechii* to breeding ponds is the primary determinant of mating opportunities (Iwasa et al. 1983, Douglas 1979, Semlitsch et al. 1993), then we expect large males to arrive at a given breeding pond earlier than small males. Small males who cannot endure harsh environmental conditions in bree-

* Corresponding author; Phone: +82-33-250-6739, e-mail: parkda@kangwon.ac.kr

ding ponds, such as freezing water and low food availability, may be forced to wait until the later part of the breeding season, when environmental conditions are milder, to enter the breeding pond. Females should tend to appear in the middle of the breeding season to increase their chances of encountering sufficient males in the breeding pond while avoiding the disadvantages of early arrival. In addition, considering that the ages of individual salamanders reflect their breeding experience (Woodrey and Chandler 1997, Dolbeer 1982, Reading 2001), older males may arrive at the breeding pond earlier than younger males. On the contrary, if the susceptibility hypothesis (Ketterson and Nolan 1983, Douglas 1979) explains the pattern of entrance of *H. leechii* to breeding ponds, then small males and females should arrive at the breeding pond earlier than large males and females, as metabolic rate and respiration rate studies suggest that large individuals have higher metabolic and respiration rates and therefore are more vulnerable to mortality resulting from long-distance migration in low temperature (Ryan and Hopkins 2000, Finkler 2006).

In this study, we determined the age structure of a *H. leechii* breeding population, analyzed relationships between the order of entrance to a breeding pond and physical parameters and age, and evaluated two competing hypotheses about the causes of variation in male and female order of entrance to the breeding pond.

MATERIALS AND METHODS

Study Site

The study site, a small pond, is located in the Research Forests of Kangwon National University (37° 46' 19", 127° 48' 56"). The pond is produced and maintained by the flow of water underground from a mountain stream, and had not run dry for at least four years prior to the study. We described the study site in detail in a previous publication (Sung et al. 2005).

Monitoring a Breeding Population

To capture salamanders entering and exiting a breeding pond, we constructed a drift fence with nine pitfall traps surrounding the pond at a 1 m distance from the edge of the pond on March 18, 2005. The nine rectangular pitfall traps (23 × 15 × 15 cm), four inside and four outside of the fence and one in the waterway of the underground stream, were buried and attached to the fence. We filled each trap with water to a 5 cm depth to prevent captured salamanders from drying and placed several leaves and two flat pebbles in each trap to provide hiding places.

A total of 16 field surveys were conducted from March 16 to April 13, 2005. Daily surveys were made between 1,600 and 2,300 h. During a survey, we checked each pitfall trap 1~4 times a day

to determine whether salamanders were caught. When salamanders were captured, we recorded the date, time, and location of capture for each individual, and measured physical parameters such as total length, SVL (snout-vent length), body mass, head length and width, and tail depth on a plastic plate dish (23 × 15 cm).

After recording physical parameters, we toe-clipped each individual for individual identification and reserved the clipped toes in 10% neutralized-formalin for a skeletochronological study. Salamanders caught in pitfall traps located outside of the fence were released inside the fence, and salamanders caught in pitfall traps inside of the fence were released outside the fence. Female salamanders caught in the trap placed on the waterway inside of the fence were classified as ovulated or oviposited based on the presence or absence of visible eggs in the abdomen, and males were classified as toe-clipped or non-clipped. Ovulated females and non-clipped males were released inside of the fence. Oviposited and toe-clipped males were released outside of the fence. When we re-captured a salamander, we treated it following the above protocol. We considered a salamander caught in a the breeding pond as an earlier arriver at the breeding site than a salamander caught in the pitfall traps if both salamanders were discovered on the same day and at the same survey time.

Skeletochronology

To prepare the clipped toes for skeletochronology in the laboratory, we followed the procedures of Hemelaar (1985). We first cleaned the clipped toes by washing them in tap water for 24 hrs and the decalcified them by submerging the toes in 5% nitric acid for 20~30 min. After another 24 hrs of washing with tap water, we paraffin-embedded the toes after a serial dehydration processes, cut them into sections at 10 μm thickness using a rotary microtome (Erma Inc. Tokyo), stained the sections using the Harris Eosin-Haematoxylin method (Presnell and Schreiber 1997), and observed them under a microscope (× 400). Growth zones and LAGs (line of arrested growth) were visible in cross sections of the phalanges (Fig. 1). The number of LAGs was counted following the methods of Leary et al. (2005). Individual age was independently estimated by the two authors. When the determinations of the two authors were different, we corroborated the LAG scores and drew a consensus conclusion.

Amphibians show an S-shaped growth curve like most ectotherms (Atkinson and Sibly 1997). We estimated the growth curve using the model of von Bertalanffy (1938) as follows: $S_t = S_m - (S_m - S_0)e^{-k(t - t_0)}$ where S_t = average body length at age t , S_m = asymptotic body length, S_0 = body length at metamorphosis, t = number of growing seasons experienced, t_0 = age at metamorphosis, and K = growth coefficient (i.e., the shape of the growth curve).

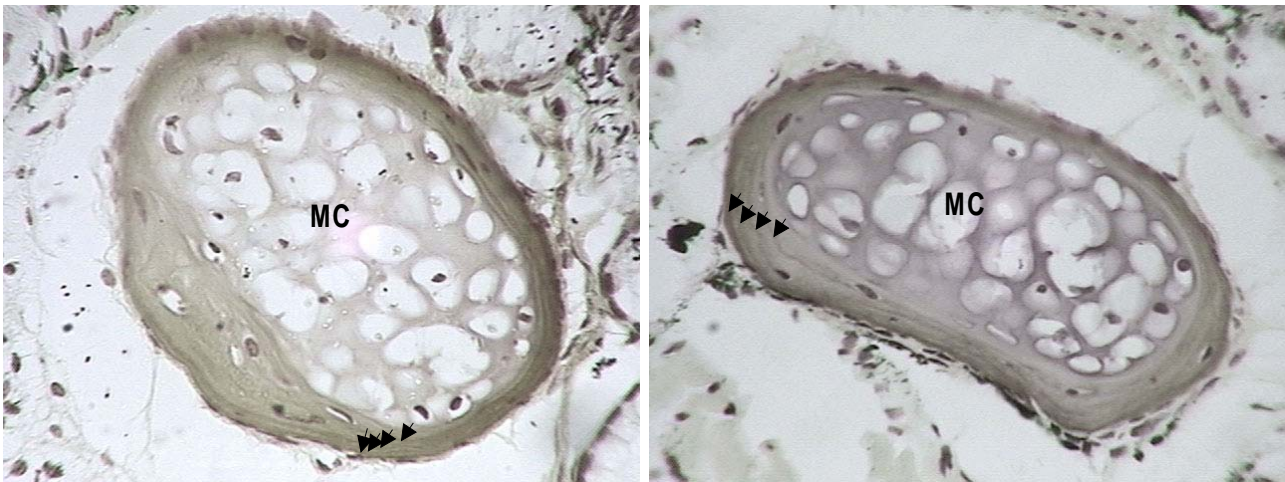


Fig. 1. Phalangeal cross sections of a 4-year-old male (left) and a 4-year-old female (right) *Hynobius leechii* from the study population. Each black arrow indicates a line of arrested growth (LAG). MC represents the medullary cavity. Magnification $\times 400$.

We estimated the age at metamorphosis as 0.3. The von Bertalanffy growth model was fitted to the average growth curves using the dynamic fitting method with SigmaPlot 10.0 (Systat Software Inc.).

Statistics

Since most data showed distributions that were not significantly different from normal (Shapiro-Wilk's normality test, $p > 0.05$, except head length and staying time), we used Pearson correlation analysis to analyze relationships among physical parameters, age, staying time, and order of entrance to a breeding pond. To compare differences between male and female physical parameters, growth coefficients and asymptotic size, we applied the independent sample t -test. Numerical data in the text are presented as mean \pm SD.

RESULTS

During the breeding season, we captured a total of 58 males and 87 females. We included in our analyses 43 males and 32 females for which age could be determined. The age of breeding males ranged from one to nine years old and most males (69.8%) were between three and five years old (Fig. 2). The asymptotic size of males was 6.36 cm and the growth coefficient was 0.71 (Fig. 3). The age of breeding females ranged from three to nine years old. The age of most females (87.5%) were between four and seven years old. The asymptotic size of females was 6.51 cm and the growth coefficient was 0.81.

The average age of breeding females was older than that of breeding males ($t = 2.24$, $df = 73$, $p < 0.028$; Table 1, Fig. 2), but the asymptotic sizes and growth coefficients of breeding males and females were not significantly different (t -test, $p > 0.05$, Fig. 3). The

SVL, body mass, and condition factor of females were greater than those of breeding males (t -tests, $p < 0.05$, Table 1), while head width and tail depth of males were greater than those of females (t -tests, $p < 0.05$, Table 1). Head length was not different between males and females (t -test, $p > 0.05$, Table 1).

Male ages showed significant positive relationships with their SVL, head length, and body mass (Table 1, Fig. 4), but female ages did not show any significant relationships with their physical parameters (Table 1, Fig. 4). There was no significant relationship between the order of entrance to the breeding pond and age for males or females. For males, the order of entrance to the breeding pond

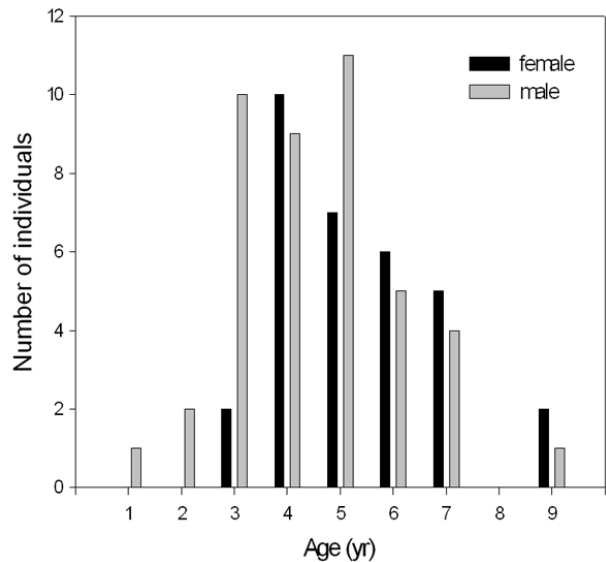


Fig. 2. Age distribution of breeding male and female *Hynobius leechii* in the study population.

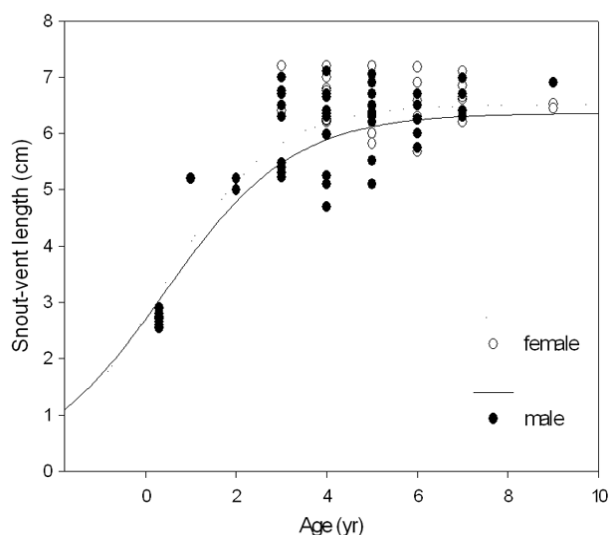


Fig. 3. Growth patterns of male and female *Hynobius leechii* in the study population, fitted to the von Bertalanffy's equation (1938). The annual growth rates and asymptotic sizes of males and females were not different.

was negatively correlated with SVL, head width, tail depth, body mass, and condition factor (Table 1, Fig. 5). For females, the order of entrance was also negatively correlated with tail depth, body mass, and condition factor, but positively correlated with SVL (Table 1, Fig. 5). Within the breeding site, males with large SVL stayed longer than smaller males, while females with small SVL stayed longer than larger females (Fig. 6).

DISCUSSION

In our study, the order of entrance to the breeding pond was not related to age, but individuals having better body condition arrived at the pond earlier. Males with larger SVL arrived earlier, while females with smaller SVL arrived earlier. These results suggest that the mate opportunity hypothesis can adequately explain the order of arrival for males at a breeding pond, whereas the susceptibility hypothesis explains some of the variation in the order of arrival for females. The different patterns for the two sexes might be caused by high intra-sexual mating competition in males and little to no intra-sexual competition for mates in females.

Amphibians that are ectotherms generally do not actively adjust their physiological condition in response to environmental changes unless the changes are critical to maintain their normal homeostasis (Brattstrom 1963). Therefore, the susceptibility hypothesis may explain the order of entrance of *H. leechii* to breeding ponds in the spring (Douglas 1979, Hasumi and Kanda 2007). In a Japanese mountain frog study, the number of times that frogs were exposed

to DCT (daily cumulative temperature, defined as the cumulative excess of temperature above a minimum threshold for the animals from a reference date) determined the time that they initiated their breeding migration (Miwa 2007). There is a possibility that *H. leechii* may also use such a mechanism. Since at low temperatures, large males and large females could face higher risk during migration than small males and females (Ryan and Hopkins 2000, Finkler 2006), the susceptibility hypothesis predicts that small individuals should enter a breeding pond earlier than large individuals. However, in our study, large males arrived at the breeding pond earlier than small males, which is not consistent with the susceptibility hypothesis. Also, both in males and females, heavier males and females and those in better body condition arrived at the breeding pond earlier, which is not consistent with the susceptibility hypothesis. However, females with small SVL arrived at the pond earlier than large females, which supports the susceptibility hypothesis. Therefore, at the moment, our result showed that the susceptibility hypothesis cannot explain the order of entrance to breeding ponds for males, but may explain in part the order of entrance for females. Hibernation in different sites may also result in different arrival patterns for males and females (Ketterson and Nolan 1976), but urodele males and females usually use similar sites for hibernation (Smith and Green 2006). Future studies should examine how individuals of different sexes and different sizes respond to environmental changes and whether their responses directly affect the order of entrance of salamanders to breeding ponds.

In our study, males with large SVL arrived at a breeding pond earlier than small males, which supports the mate opportunity hypothesis. Larger males with better body condition arrived early at the breeding pond and stayed longer within the pond. This behavior may allow large males to have more opportunities to mate than later-arriving and shorter-staying small males. Since food is very limited in the breeding pond during the breeding period (Park and Park 2000, Sung et al. 2005), large individuals with more energy stored may be able to stay in the pond longer than small individuals, who have relatively little usable stored energy. Since there is higher risk in the early breeding season for failed fertilization and freezing, and the late breeding season is characterized by the presence of a greater proportion of small, lower-quality males, better-conditioned females might be predicted to arrive in the middle of the breeding season. However, in our study, better conditioned, but small females arrived at the breeding pond early, which is not consistent with our expectation, suggesting that female arrival pattern does not follow the predictions of the mate opportunity hypothesis. Furthermore, age of males and females did not show significant relationships with the order of entrance to the breeding pond, suggesting that other factors that were not consi-

Table 1. Relationships among physical parameters, age, and order of entrance to the breeding pond for breeding male and female *Hynobius leechii*. a, Pearson correlation coefficient (r); b, Type I error probability (P); *, $P < 0.05$. The sample size for the staying time was $N = 26$ and all other sample sizes were $N = 43$ for males and $N = 32$ for females.

	SVL	Head length	Head width	Tail depth	Body mass	Condition factor	Staying time	
Male	Head length	0.594 ^a 0.000 ^{b*}						
	Head width	0.672 0.000 [*]	0.607 0.000 [*]					
	Tail depth	0.398 0.008 [*]	0.165 0.291	0.486 0.001 [*]				
	Body mass	0.648 0.000 [*]	0.416 0.006 [*]	0.684 0.000 [*]	0.704 0.000 [*]			
	Condition factor	0.236 0.128	0.154 0.323	0.459 0.002 [*]	0.637 0.000 [*]	0.882 0.000 [*]		
	Staying time	0.437 0.026 [*]	-0.184 0.369	0.247 0.225	0.338 0.092	0.226 0.267	0.018 0.931	
	Age	0.406 0.007 [*]	0.438 0.003 [*]	0.182 0.244	-0.004 0.978	0.328 0.032 [*]	0.179 0.250	-0.091 0.658
	Order of entrance to the pond	-0.431 0.004 [*]	-0.079 0.615	-0.406 0.007 [*]	-0.660 0.000 [*]	-0.474 0.001 [*]	-0.346 0.023 [*]	-0.609 0.001 [*]
Female	Head length	0.071 0.701						
	Head width	0.629 0.000 [*]	0.053 0.773					
	Tail depth	-0.142 0.437	0.006 0.974	0.212 0.243				
	Body mass	0.256 0.157	0.067 0.714	0.234 0.197	0.399 0.024 [*]			
	Condition factor	-0.098 0.595	0.040 0.830	0.028 0.877	0.476 0.006 [*]	0.936 0.000 [*]		
	Staying time	-0.556 0.003 [*]	-0.179 0.382	-0.311 0.122	0.265 0.191	0.287 0.155	0.494 0.010 [*]	
	Age	-0.035 0.851	0.216 0.236	-0.050 0.788	0.028 0.881	0.041 0.822	0.040 0.828	-0.239 0.239
	Order of entrance to the pond	0.443 0.011 [*]	0.063 0.732	-0.050 0.788	-0.589 0.000 [*]	-0.559 0.001 [*]	-0.743 0.000 [*]	-0.735 0.000 [*]

dered in this study affect the order of entrance of *H. leechii* to breeding ponds. Future studies should attempt to clarify whether variation in the size of males and females is correlated with variation in mating success, and if so, whether the relationship is mediated by their order of arrival at the breeding pond over the breeding period.

Tail depth is believed to be a good indicator of body condition for breeding male and female *H. leechii*. In urodeles, the tail is one of the sites used for storage of nutrients. The tail depth is regulated by sex hormones and prolactin (Dent 1975) and in conditions of food deprivation the tail depth greatly decreases (Pool and Dent 1977). In our study, tail depth was correlated with male and female

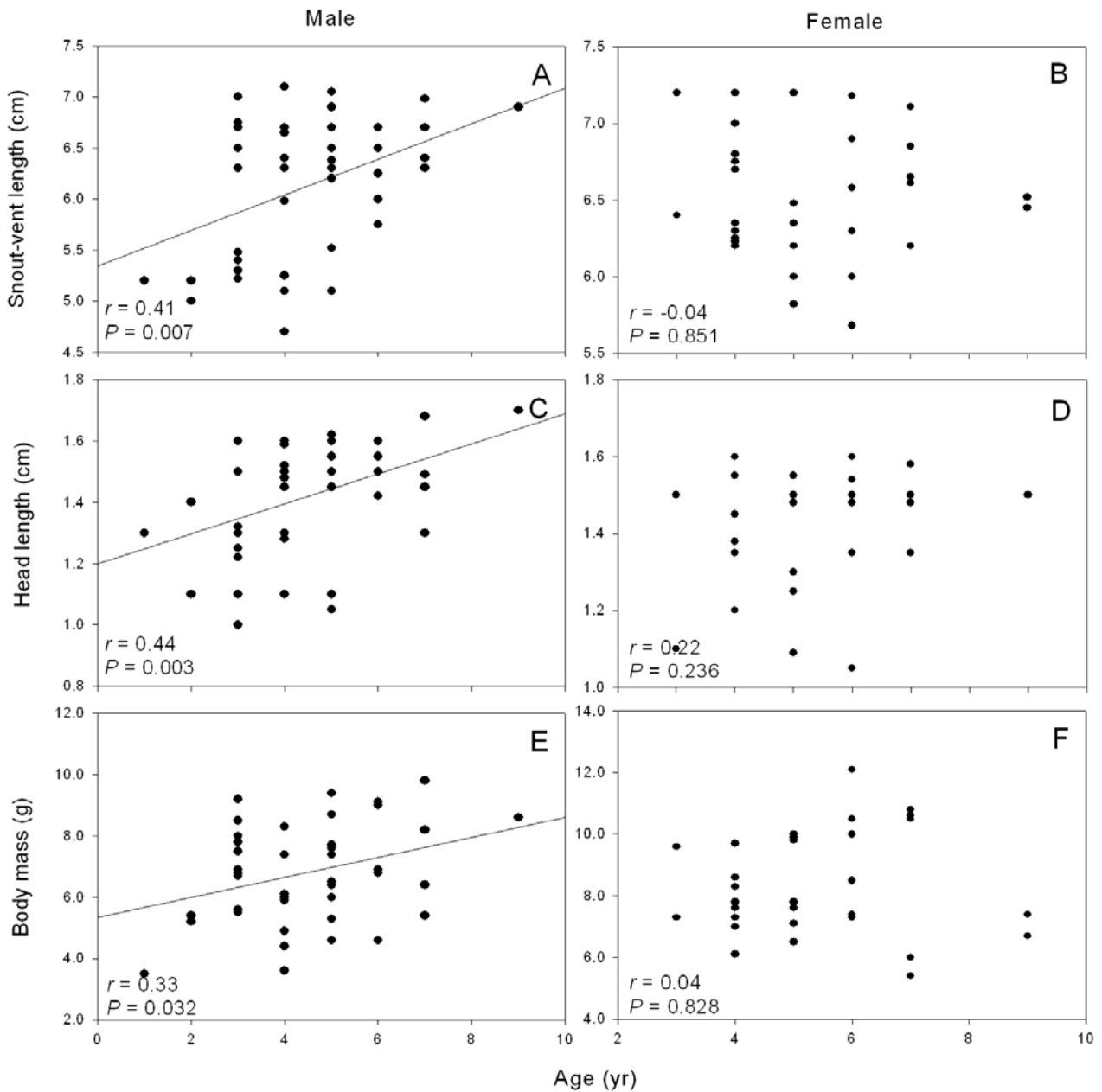


Fig. 4. Relationships between age and physical parameters for males (A, C, E) and females (B, D, F). Males' snout-vent length (SVL, A), head length (C), and body mass (E) were positively correlated with their age, whereas no physical parameter of females was significantly correlated with their age.

condition factors, meaning that salamanders having a greater tail depth are healthier. Also, the order of entrance to the breeding pond showed a strong negative correlation with the tail depth, suggesting that males and females having a greater tail depth arrived at the pond earlier and stayed longer. Jeon et al. (2005) showed that tail depth in Korean salamanders affects the generation of water vibrations which are used in intra-sexual competition. It would be interesting to know whether the tail depth is responsible for the qua-

lity of mating signals of male salamanders.

Our study is the first to determine the age structure of a urodele population in Korea. However, several previous studies have determined the age structures of other *Hynobius* breeding populations. Ento and Matsui (2002) reported that the youngest individuals observed mating were four-year-old males and five-year-old females of *H. nebulosus*, whereas five-year-old males and seven-year-old females were the youngest *H. kimurae* to reproduce (Misawa and

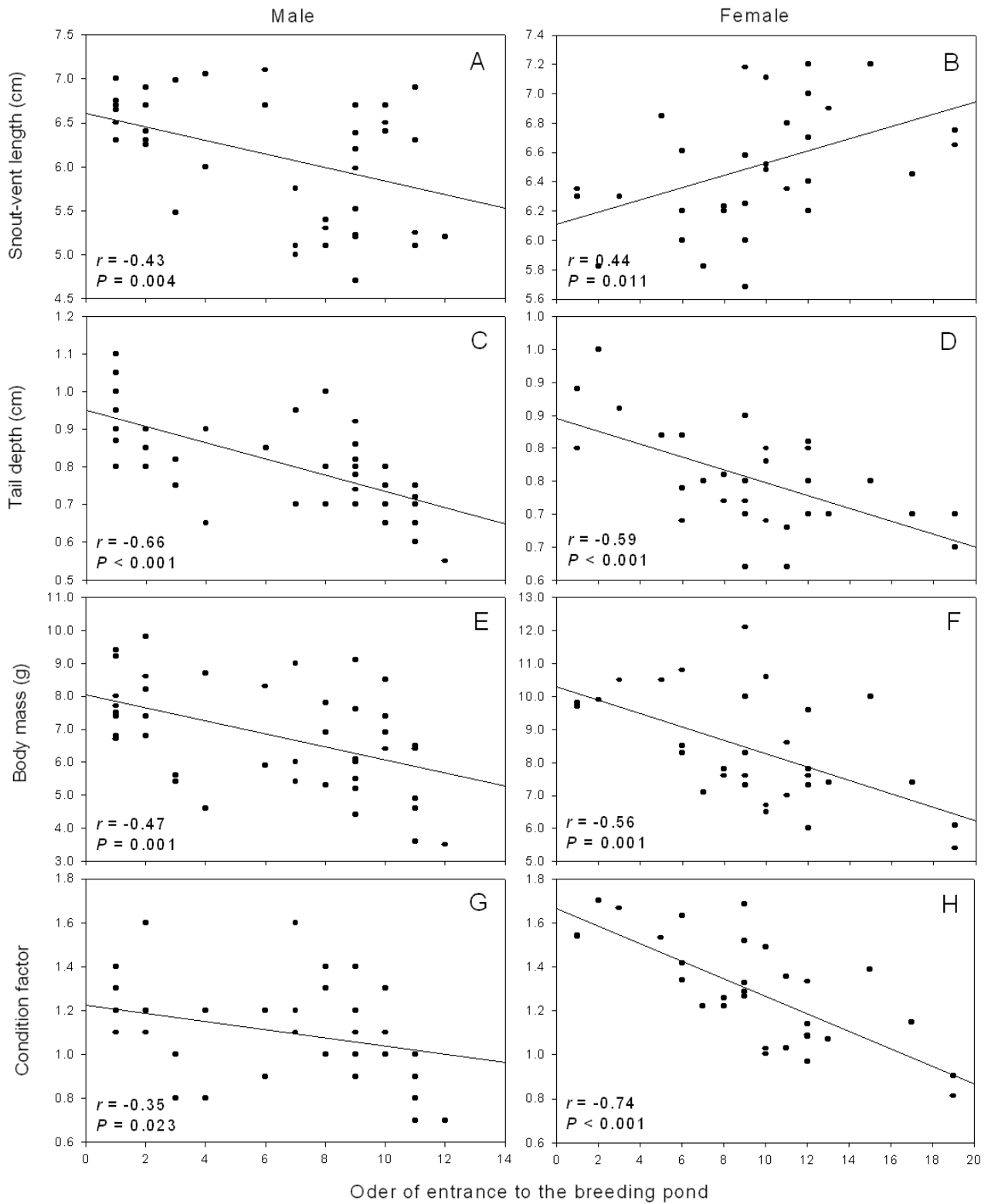


Fig. 5. Relationships between the order of entrance to the breeding pond and male (A, C, E, G) and female (B, D, F, H) physical parameters. The tail depth, body mass, and condition factor of both males (C, E, G) and females (D, F, H) showed significant relationships with the entering order. Male's snout-vent length (SVL, A) was negatively correlated with the order of entrance, but female's SVL (B) was positively correlated with the order of entrance.

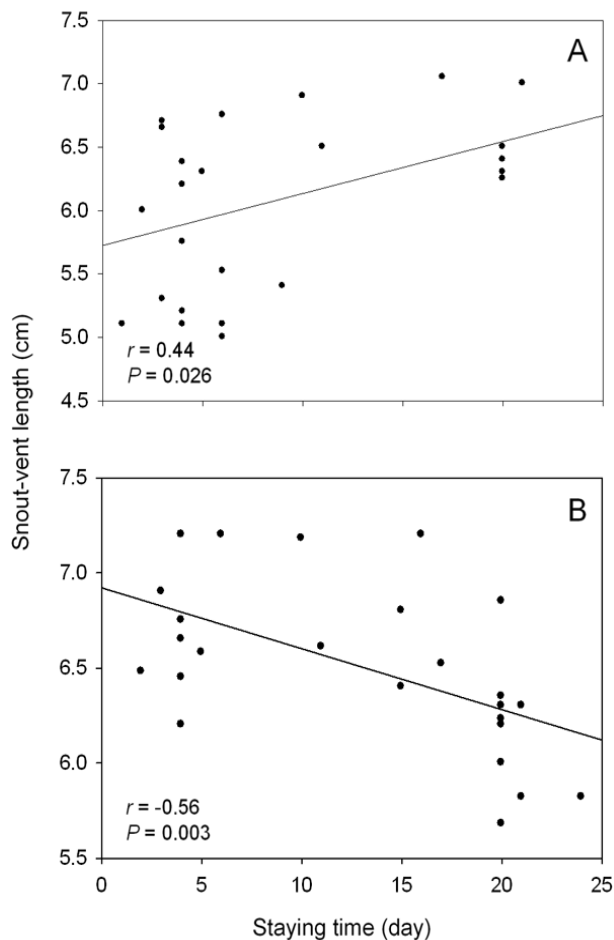


Fig. 6. Relationships between the staying time in the breeding pond or at the breeding site and the snout-vent length (SVL) of breeding male (A) and female (B) *Hynobius leechii*. Larger males stayed at the pond longer, while smaller females stayed at the breeding site longer.

Matsui 1999). In our study, one-year-old male and three-year-old females were observed mating. These differences may result from methodological problems, as several studies have reported difficulties in determining the age of amphibians using skeletochronology (Hemelaar 1985, Wake and Castanet 1995, Eden et al. 2007, Lee et al. 2008). However, to date, skeletochronology is still considered to be the most reliable method to determine the ages of amphibians, and is used by many researchers (Trenham et al. 2000, Ento and Matsui 2002).

In conclusion, our study suggests that intra-sexual mating competition may shape the pattern of arrival of male *H. leechii* at breeding ponds and that body condition, such as the amount of stored energy, may also affect their immigration schedule. Our study is the first to determine the age structure of a urodele breeding population in Korea.

ACKNOWLEDGMENTS

We thank Ji-Yeong Lee, Sang-Kyu Park, Jae-Ok Shim, Hyeon-Jeong Park and Sang-Heon Han for their help with the field work. This study was supported by a grant (R01-2004-000-10450-0) from the Basic Research Program of the Korea Science & Engineering Foundation.

LITERATURE CITED

- Atkinson D, Sibly RM. 1997. Why are organisms usually bigger in colder environments? Making sense of a life-history puzzle. *Trends Ecol Evol* 12: 235-239.
- Brattstrom BH. 1963. A preliminary review of the thermal requirements of amphibians. *Ecology* 44: 238-255.
- Dent JN. 1975. Integumentary effects of prolactin in the lower vertebrates. *Amer Zool* 15: 923-935.
- Dolbeer RA. 1982. Migration patterns for age and sex classes of black-birds and starlings. *J Field Ornithol* 53: 28-46.
- Douglas ME. 1979. Migration and sexual selection in *Ambystoma jeffersonianum*. *Can J Zool* 57: 2303-2310.
- Eden CJ, Whiteman HH, Duobinis-Gray L, Wissinger SA. 2007. Accuracy assessment of skeletochronology in the Arizona tiger salamander (*Ambystoma tigrinum nebulosum*). *Copeia* 2007: 471-477.
- Ento K, Matsui M. 2002. Estimation of age structure by skeletochronology of a population of *Hynobius nebulosus* in a breeding season (Amphibia, Urodela). *Zool Sci* 19: 241-247.
- Finkler MS. 2006. Effects of temperature, sex, and gravidity on the metabolism of small-mouthed salamanders, *Ambystoma texanum*, during the reproductive season. *J Herpetol* 40: 103-106.
- Gauthreaux SA Jr. 1978. The ecological significance of behavioral dominance. In: *Perspectives in Ethology*, Vol 3 (Bateson PPG, Klopfer PH, eds). Plenum Press, New York, pp 17-54.
- Hasumi M, Kanda F. 2007. Phenological activity estimated by movement patterns of the siberian salamander near a fen. *Herpetologia* 63: 163-175.
- Hemelaar A. 1985. An improved method to estimate the number of year rings resorbed in phalanges of *Bufo bufo* and its application to populations from different latitudes and altitudes. *Amphibia-Reptilia* 6: 323-341.
- Iwasa Y, Odendaal JF, Murphy DD, Ehrlich PR, Launer AE. 1983. Emergence patterns in male butterflies: a hypothesis and a test. *Theor Pop Biol* 23: 363-379.
- Jeon JK, Ji CS, Park DS. 2005. Water vibrations play role in male-male competition of *Hynobius leechii*. *Integ Biosci* 9: 156
- Ketterson ED, Nolan VJ. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis hyemalis*). *Ecology* 57: 679-693.
- Ketterson ED, Nolan VJ. 1983. The evolution of differential bird migration. In: *Current Ornithology*, Vol 1 (Johnston RF, ed). Plenum Press, New York, pp 357-402.
- Leary CJ, Fox DJ, Shepard DB, Garcia AM. 2005. Body size, age, growth and alternative mating tactics in toads: satellite males are

- smaller but not younger than calling males. *Anim Behav* 70: 663-671.
- Lee JH, Ra NY, Eom JH, Park D. 2008. Population dynamics of the long-tailed clawed salamander larva, *Onychodactylus fischeri*, and its age structure in Korea. *J Ecol Field Biol* 31: 31-36.
- Lodé T, Holveck MJ, Lesbarrères D. 2005. Asynchronous arrival pattern, operational sex ratio and occurrence of multiple paternities in a territorial breeding anuran, *Rana dalmatina*. *Biol J Linn Soc* 86: 191-200.
- Misawa Y, Matsui M. 1999. Age determination by skeletochronology of the Japanese Salamander, *Hynobius kimurae* (Amphibia, Urodela). *Zool Sci* 16: 845-851.
- Miwa T. 2007. Conditions controlling the onset of breeding migration of the Japanese mountain stream frog, *Rana sakuraii*. *Naturwissenschaften* 94: 551-560.
- Morbey YE, Ydenberg RC. 2001. Protandrous arrival timing to breeding areas: a review. *Ecol Lett* 4: 663-673.
- Park D, Park SR. 2000. Multiple insemination and reproductive biology of *Hynobius leechii*. *J Herpetol* 34: 594-598.
- Park SR, Park DS, Yang SY. 1996. Courtship, fighting behaviors and sexual dimorphism of the salamander, *Hynobius leechii*. *Korean J Zool* 39: 437-446.
- Pool TB, Dent JN. 1977. Ultrastructure and hormonal control of product synthesis in hedonic glands of red-spotted newt, *Notophthalmus viridescens*. *J Exp Zool* 201: 177-201.
- Presnell JK, Schreibman MP. 1997. *Humason's Animal Tissue Techniques*. Johns Hopkins University Press, Baltimore, pp 101-118.
- Reading CJ. 2001. Non-random pairing with respect to past breeding experience in the common toad (*Bufo bufo*). *J Zool* 255: 511-518.
- Ryan TJ, Hopkins WA. 2000. Interaction of sex and size and the standard metabolic rate of paedomorphic *Ambystoma talpoideum*: size does matter. *Copeia* 2000: 808-812.
- Semlitsch RD, Scott DE, Pechmann J, Gibbons JW. 1993. Phenotypic variation in the arrival time of breeding salamanders: individual repeatability and environmental influences. *J Anim Ecol* 62: 334-340.
- Smith AM, Green DM. 2006. Sex, isolation and fidelity: unbiased long-distance dispersal in a terrestrial amphibian. *Ecography* 29: 649-658.
- Sung HC, Lee JH, Park D. 2005. Entering and exiting routes of *Hynobius leechii* to a breeding site and staying time within the site. *Korean J Ecol* 28: 237-243.
- Trenham PC, Shaffer HB, Koenig WD, Stromberg MR. 2000. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). *Copeia* 2000: 365-377.
- von Bertalanffy L. 1938. A quantitative theory of organic growth. *Hum Biol* 10: 181-213.
- Wake DB, Castanet J. 1995. A skeletochronological study of growth and age in relation to adult size in *Batrachoseps attenuatus*. *J Herpetol* 29: 60-65.
- Wang G, Greenfield MD, Shelly TE. 1990. Inter-male competition for high-quality host-plants: the evolution of protandry in a territorial grasshopper. *Behav Ecol Sociobiol* 27: 191-198.
- Wiklund C, Solbreck C. 1982. Adaptive versus incidental explanations for the occurrence of protandry in a butterfly, *Leptidea sinapis* L. *Evolution* 36: 56-62.
- Woodrey MS, Chandler CR. 1997. Age-related timing of migration: geographic and interspecific patterns. *Wilson Bull* 109: 52-67.

(Received May 27, 2008; Accepted July 25, 2008)