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Research paper

Seasonal changes in body shape and mass in a lotic-breeding and externally fertilizing salamander *Hynobius kimurae*

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ABSTRACT

Physiological condition linked to reproduction-related morphological traits (e.g., body mass, head width, tail height) is a key determinant of ecotypes related to fitness in ecological selection. In migratory salamanders such as the families Ambystomatidae (internal fertilization), Salamandridae (internal), and Hynobiidae (external), such morphological traits change at the transition between terrestrial and aquatic habitats. Unlike many other migratory salamanders, *Hynobius kimurae* (Hynobiidae) immigrates from land to water for aquatic hibernation during fall, and the immigration is not related to fall breeding. In this context, does fall immigration to water for winter dormancy induce changes in reproduction-related morphological traits? We analyzed changes in body shape and mass concurrent with physiological condition of 244 males and 131 females of *H. kimurae* with only data on first capture during fall and spring from 1996 to 2016. Although reproduction-related morphological traits in other migratory salamanders change simultaneously when they enter the water and subsequently initiate breeding during either season of fall–spring, such changes occurred both in male and female *H. kimurae* firstly during fall (shortly after entering the water) and secondly during spring (shortly after awaking from hibernation), except for head width being static throughout seasons. The differences suggest that these two-step changes during a prolonged period from fall to spring would be concentrated in a short period of breeding activity during either season of fall–spring in other migratory salamanders without hibernating in the water. As sexually selected, sexual dimorphism was detected in size and shape, especially shape of the tail, both height and length of which were greater in males than in females regardless of the sexes being terrestrial or aquatic. The male's larger tail during the terrestrial phase may be a stock for a more developed tailfin (amount of reproductive output) in the aquatic-phase male potentially related to fitness.

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1. Introduction

Many animals show sexual dimorphism, which is determined by sexual selection, ecological selection, and/or fecundity selection and thus is an eternal theme for evolutionary biologists (Darwin, 1888; Slatkin, 1984; Andersson, 1994). Under sexual selection, phenotypic intersexual differences usually occur because sexual differences play an important role in breeding with favorable selection evolving reproduction-related morphological traits that permit either sex to gain a better mate; under ecological selection, sexual competition induces niche divergence or divergence in reproduction-related morphological traits between the sexes

(Shine, 1989; Malmgren, 2001; Kupfer, 2007). Since physiological data to link ecotypes with fitness have been hypothesized to support ecological selection (Pratchett et al., 2012), physiological condition linked to reproduction-related morphological traits (Hasumi and Iwasawa, 1990) should be a major determinant of individual fitness in ecological selection.

A study of sexual dimorphism specially focuses on size (i.e., sexual size dimorphism: SSD), generally with female-larger SSD in salamanders (Shine, 1989; Kupfer, 2007), but sometimes focuses on shape (Malmgren and Thollessen, 1999; Hasumi, 2010). In hynobiid salamanders changes in body shape and mass co-occur drastically with the physiological condition at the transition in terrestrial- and aquatic-phase morphs during spring breeding regardless of lentic-breeding habits (e.g., *Hynobius retardatus*: Aoto, 1950; *H. nigrescens*: Hasumi and Iwasawa, 1990; Hasumi, 1994; *Salamandrella keyserlingii*: Hasumi and Borkin, 2012) or lotic-breeding habits (*Onychodactylus japonicus*: Akita, 2009). In case of male-

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biased SSD (found in *H. nigrescens*), male–male competition has been proposed to enhance increased head width (HW: Hasumi, 1994; Alcorn et al., 2013). In case of female-biased SSD (present in *S. keyserlingii*), the swelling of the whole body of small-sized males, including increased HW, has been hypothesized to develop temporarily during aquatic breeding when engaging in spawning (i.e., simultaneous extrusion of sperm and oviposition) coincident with large-sized females to resolve intersexual ontogenetic conflict (Hasumi, 2010, 2015). This conflict is characterized by alleles beneficial to one sex but harmful to the other (e.g., Badyaev, 2002).

Increased male HW during aquatic breeding, i.e., a reproduction-related morphological trait resulted from the swelling of the whole body, is unknown in salamander families other than the Hynobiidae (Hasumi and Iwasawa, 1990; for a review, see Hasumi, 2015). For example, in aquatic-breeding salamandrids, body mass increases, and a tailfin develops, but HW does not increase at all (Mazzi and Vellano, 1987). In aquatic-breeding *Triturus cristatus* or *T. marmoratus*, a crest-like dorsal fin develops in males, but HW shows no intersexual difference (Malmgren, 2001; Reinhard and Kupfer, 2015). Male-biased sexual dimorphism occurs in relative HW of aquatic plethodontid salamanders, *Eurycea aquatica* and *E. cirrigera*, but this difference is seasonally constant (Alcorn et al., 2013). In migratory salamanders such as ambystomatids (internal fertilization), salamandrids (internal fertilization), and hynobiids (external fertilization), changes in these traits concur with breeding activity in the water during either season of fall–spring (Wells, 2007; Hasumi, 2015; Pough et al., 2015). There exist fall breeders such as ambystomatids (*Ambystoma talpoideum*: Krenz and Sever, 1995; *A. macrodactylum*: Verrell, 2004; *A. annulatum*: Anderson et al., 2015) and salamandrids (*Notophthalmus viridescens*: Healy, 1975; *N. perstriatus*: Johnson, 2002). A hynobiid species *Hynobius abei* breeds in the mud always during winter (around December: Sato, 1934).

Lotic-breeding *Hynobius kimurae* move to aquatic hibernacula during fall, in which males and females overwinter in a water stream under the snow until awakening in spring for breeding (Akita, 2001; Akita and Miyazaki, 2009; Kakegawa and Hasumi, Unpublished results). Aquatic hibernation in *H. kimurae* would be unlikely in other migratory salamanders (Kakegawa and Hasumi, Unpublished results). Fall immigration toward terrestrial hibernacula near a body of fen water is known in *S. keyserlingii*, but this species does not enter the water during fall (Hasumi and Kanda, 2007). Because changes from terrestrial-phase morphs to aquatic-phase morphs in *H. kimurae* highly depend on changes in body size parameters during fall and spring, showing these changes is of quite significance for considering their relationships with physiological adaptation to aquatic environments, which is an evolutionary determinant of individual fitness in ecological selection (Pratchett et al., 2012), or with reproductive parameters such as spermiation (defined here as sperm release from the testis into the vas deferens: e.g., Hasumi et al., 1990; Yartsev and Kuranova, 2015), sperm storage, and sperm evacuation in males and ovulation, egg sac formation, and oviposition in females (see Hasumi, 2015).

In this context, specific research questions were as follows. (1) In *H. kimurae*, like other hynobiids, do changes in body shape and mass occur immediately after males and females submerge into water for hibernation during fall? (2) If these changes occur, how do they coincide with changes in reproductive parameters during spring? (3) If those changes do not occur, when do they occur during winter dormancy and the succeeding spring breeding? (4) How are changes in body shape and mass different from those of other hynobiids? (5) Does sexual dimorphism in body shape and mass occur not only in aquatic-phase morphs but also in terrestrial-phase morphs? To address these questions, we investigated changes in body shape and mass in 244 males and 131 females of *H. kimurae* using only data on first capture during fall and spring from 1996 to 2016 with respect to environmental condition (e.g., terres-

trial, aquatic) and physiological condition (e.g., spermiation, sperm storage, ovulation, egg sac formation).

2. Materials and methods

2.1. Study area and animals

From October 1996 to May 2016, we captured a total of 279 males and 144 females of the lotic-breeding *Hynobius kimurae* around a water stream, 119.7 m-long, on the forest floor of Mt. Sengen-yama, in the northern part of Hakuba-mura, Nagano Prefecture, Japan (36.73° N, 137.88° E; 840 m elevation). Because adults of lotic-breeding hynobiids cannot easily be captured even during the aquatic phase, obtaining enough specimens for morphometric comparisons was quite time-consuming. From our long-term field surveys we estimated mean water temperature of 6°C for the stream at the start of the breeding season in mid-March when the stream was occasionally covered with deep snow. Unlike other migratory salamanders, *H. kimurae* annually moved to aquatic hibernacula during fall, and both sexes overwintered in stream water at around 2°C under the snow cover until spring breeding. The mean duration of staying in water was estimated 21.7 weeks in males and 19.0 weeks in females (Kakegawa and Hasumi, Unpublished results).

We distinguished gravid females from males on the basis of yellowish maturing follicles in the ovaries, as well as beige oviducts and ovisacs (i.e., homologous uteri: see Hasumi, 1996), being visible through the skin of the ventral side of the trunk (e.g., Hasumi and Borkin, 2012). We further used sexual dimorphism of hindlimbs and cloacae for identifying sexes independently of gravid or spent females. We examined the absence or presence of sperm in the vasa deferentia of each male (i.e., spermiation and thus sperm storage) by checking sperm emanated from the cloacal opening after pressing the lateral region of the trunk. We estimated ovulation in females by checking the presence of oviductal ova externally visible through the skin of the ventral side of the trunk.

We used noninvasive photographs of a dorsal side of each captured individual for identification by means of an ontogenetically constant pattern of dorsal yellow spots after metamorphosis (Kakegawa and Hasumi, Unpublished results). However, for 20 years, we obtained only 35 male and 13 female recaptures (two times or more) among the 279 males and 144 females. To ensure independence of data and to avoid multiple measurement or pseudoreplication, we included only data on first capture for analyses (males: $n = 244$; females: $n = 131$).

2.2. Capture categories

We categorized the 244 males into seven classes (Table 1):

- (1) MFT ($n = 85$): immigrating males captured under cover objects (e.g., downed logs, woody debris, leaf litter, moss mats) at 0.5–8.0 m distances from the stream on the forest floor during October–November;
- (2) MFE ($n = 7$): presumably land–water wandering males captured at 50–70° slopes of a 30 cm distance from the stream during October–November (wandering = frequent movement in and out of the water before aquatic adaptation: see Hasumi and Iwasawa, 1992);
- (3) MFA ($n = 65$): males shortly after entering the stream for aquatic hibernation during November–December;
- (4) MSA1 ($n = 10$): prebreeding males after spermiation and thus during sperm storage in the vasa deferentia at the cessation of hibernation in the stream during March (in captivity, spermiation begins 13.8 weeks in average after males enter the water

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