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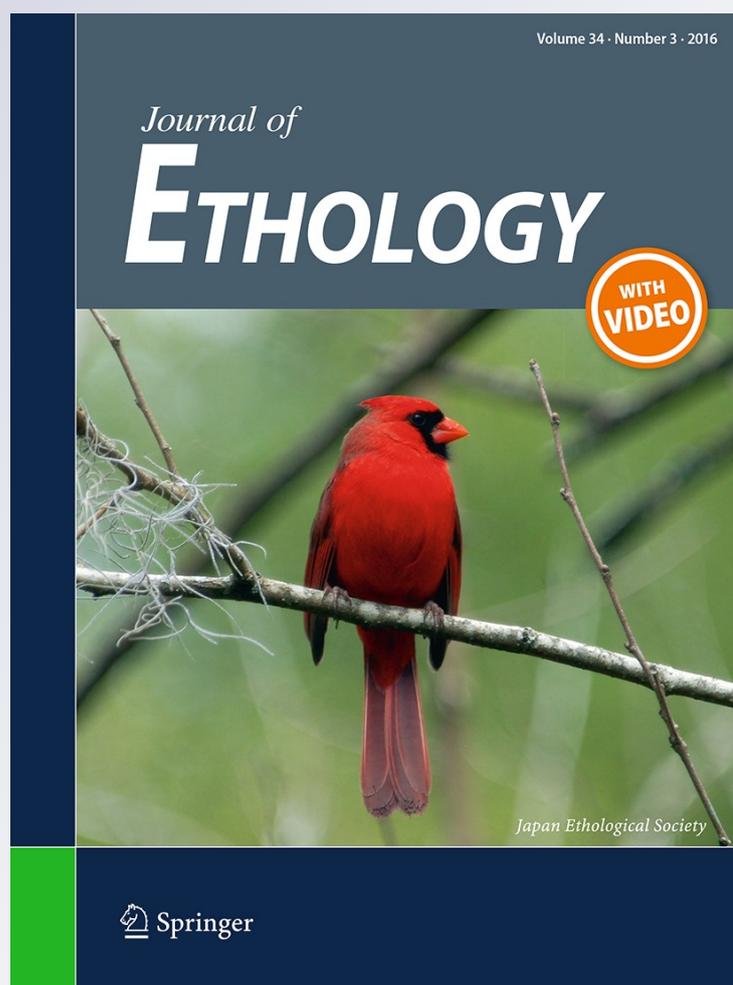
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Female preference for both behavior and morphology traits of the male Japanese newt *Cynops pyrrhogaster*

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Abstract Males of the Japanese newt (*Cynops pyrrhogaster*) display complex courtship behaviors and are sexually dimorphic in terms of tail morphology. Pair encounter experiments were conducted to investigate which males are preferred by female newts. Male courtship behavior consisted of four stages, namely, Approach, Fan, Creep and Spermatophore deposition. The Fan behavior was classified into four sub-patterns. Males which showed a specific sub-pattern were accepted at a significantly higher probability by females than males which showed the other sub-patterns. The accepted males had a smaller snout–vent length, higher tail, and larger body mass than the rejected males, and their body weight was relatively heavier. Our results suggest that females of *C. pyrrhogaster* select their mates based on both behavioral patterns and morphological characters.

Keywords Female preference · Sexual selection · Newt · Mating behavior · Sexual dimorphism

Introduction

Males of many animal species have more than a single exaggerated secondary sexual trait (Møller and Pomiankowski 1993; Young et al. 1994; Gibson and Landen 1996; Marchetti 1998). For example, males of the American sage grouse *Centrocercus urophasianus* weigh twice as

much as females and possess an elaborate plumage, large esophageal pouches and air sacs that are lacking in the females (Young et al. 1994). Secondary sexual traits have been attributed to the effects of sexual selection because the presence of exaggerated sexual traits is apparently not advantageous to survival (Darwin 1871; Andersson 1994). Some traits, such as antlers, spurs and horns, are obviously used in male–male competition. Other traits, such as the extravagant feather plumes of many birds, are regarded as sexual signals that are used by females to choose a mate (Møller and Pomiankowski 1993).

Male newts produce multimodal signals to attract females, and several different mechanisms could result in the evolution of multiple male sexual traits. First, the traits used in male–male competition may differ from those which form the basis of female choice (Marchetti 1998). Second, females can assess several male traits simultaneously, all of which indicate male quality, and may make their decisions based on a combination of traits (Marchetti 1998; Freeman-Gallant et al. 2010; Kekäläinen et al. 2010). Third, different male traits may indicate different aspects of male quality, such as short- versus long-term condition (Møller and Pomiankowski 1993). Fourth, different male traits may be used at different mating stages: finding, assessing and selecting a mate (Gibson 1996; Luttbeg et al. 2001). Fifth, the use of multimodal signals may be beneficial in heterogeneous environments (Secondi et al. 2015).

Males of the Japanese newt (*Cynops pyrrhogaster*) have multiple secondary sexual traits. Courtship behavior is composed of multiple stages (Kawamura and Sawada 1959). Although *C. pyrrhogaster* males frequently court females, most attempts are rejected (Sawada 1963b). The tails of newts show sexual dimorphism, i.e. the male's tail is higher and shorter than that of the female. *C. pyrrhogaster* females can choose their mates using either or both courtship

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behavior and tail size. In addition, in *C. pyrrhogaster* there is geographic variation in both courtship behavior and morphological characters (Sawada 1963a, b). Genetic differentiations among populations have also been detected (Hayashi and Matsui 1988, 1990; Tominaga et al. 2013).

There is, however, no information on how *C. pyrrhogaster* females select mates, although such information is crucial to an understanding of the importance of sexual traits. We have recorded courtship behavior in a single population of *C. pyrrhogaster* as a first step to improving our understanding of the evolution of multiple sexual traits in this species. We also examined how courtship behavior and sexually dimorphic morphological characters affect the outcome of female acceptance in each stage, and whether these traits act in combination or independently of each other.

Materials and methods

Study organism

Cynops pyrrhogaster is a member of the family Salamandridae and can be found in Japan from Northern Honshu to Kyushu. Individuals are mainly black, but have a red background coloration and black blotches on the ventral body surface. Many individuals aggregate in ponds during the breeding seasons. The breeding seasons fall in the spring (April–July) and fall (October–November), but eggs are laid only in the spring (Hayashi 1996). Females mate more than once in a breeding season (T. Kutsuki, unpublished data) and can store sperm in their spermathecae from the fall to the following spring (S. Akiyama, personal communication). During the breeding seasons, males show nuptial coloring, which consists of blue and purple coloring on the lateral sides of the body and tail (Sawada 1963a; Hayashi 1996). Although a recent study showed that a male newt's sexual attractiveness is influenced by UV wavelengths (Secondi et al. 2012), the effect of this character was not assessed in the present study due to the lack of equipment needed to quantify the strength of UV radiation. Males display courtship behavior under the water (Kawamura and Sawada 1959). Females lay eggs separately on fallen leaves and/or grass roots under the water, and these are all individually fertilized when they pass through the spermatheca. Females may lay anywhere from a few to 40 eggs in a single session and between 100 and 400 eggs in total during a breeding season (Hayashi 1996).

Sampling and rearing conditions

In mid-April and early October 2001, we collected 75 males and 52 females of *C. pyrrhogaster* from a rice field

in Hamakanaya, Chiba Prefecture, Japan. Although it was not possible to establish whether the individuals were virgin or not, we collected them very early in the breeding season and therefore assumed that the females had not yet mated that year. The collected individuals were taken to Hokkaido University and divided over six containers (73 × 45 × 24 cm), with 20 individuals per container. The containers were filled with water to a depth of 5–10 cm, and a piece of polystyrene (15 × 15 cm) and several water-weeds were provided as perches and shelters. Water temperature was kept between 15 °C and 25 °C. All individuals were kept in the laboratory until the end of the experiments and then returned to the collection site. It was possible to recognize all newts individually by the distinctive patterns of black spots on their ventral surfaces. In this study, we adhered to the 'Guidelines for the use of animals in research' (Animal Behavior Society 1991).

Morphological measurements

We measured snout–vent length (from the tip of the snout to the anterior end of cloaca; SVL), tail length (from the anterior end of cloaca to the tip of tail; TL) and tail height at the deepest section of the tail (TH) of all individuals to the nearest 1.0 mm. Body mass (W) was measured soon after the collection to the nearest 1.0 g. Each character was measured three times within 4 h, and the average values were used in analyses. Statistical analyses were conducted using StatView 5.0 (SAS Institute, Raleigh, NC) and SPSS version 11.5 (IBM Corp., Armonk, NY).

Experiments

Behavioral observations were conducted during the two breeding seasons of 2001 (from mid-April to June, and from mid-October to early November). Pairing encounter experiments were conducted in glass tanks (60 × 29.5 × 36 cm) filled with water to a depth of 7 cm. The water temperature was maintained at 20 °C. Before each experiment the glass tank was divided into two sections using a black plastic board, and in each section either a male or a female (together a male/female pair) was introduced for approximately 24 h before the start of an observation. After removing the partition, we observed the behavior of both individuals for 30 min using video cameras (digital video cameras: model NV-DE3, Panasonic, Osaka, Japan; model SR-S970, Victor, Kanagawa, Japan). The recordings were conducted under the dark condition in the absence of short-wavelength light; thus, we did not examine the effect of the nuptial color of males in our experiments. After each experiment, the tanks were flushed with water to remove any chemical traces from the animals in the previous test that may influence the following test.

Females that picked up spermatophores were not used in any further experiments because female mating preferences change with successive mating in the smooth newt (*Triturus vulgaris*) (Gabor and Halliday 1997).

Behavioral observations

The sexual behavior displayed by *C. pyrrhogaster* can be defined into the sequential stages presented in the following list [with the behavioral sequence of each sex denoted by numerals, such as (male 1), (male 2), (female 1)] (Kawamura and Sawada 1959; Sparreboom and Ota 1995; Hayashi 1996; Sparreboom 1996; see also Fig. 1):

- I. (Male 1) Approach. A male approaches a female. The male sniffs the female's lateral body or cloaca.
- II. (Male 2) Fan. The male bends its tail to the side facing the female and makes rapid vibrating movements with the tip of the tail.
- III. (Female 1) Push. The female responds to the male's courtship by pushing the male's neck with its snout.

IV. (Male 3) Creep. This behavior represents a distinct phase in the courtship sequence. The male turns away from the female and creeps with an undulating tail ahead of it at a slow pace.

V. (Female 2) Follow. The female follows directly behind the male.

VI. (Female 3) Touch. The female follows the male's undulating tail and touches it with her snout.

VII. (Male 4) Spermatophore deposition. A spermatophore is deposited in the water during the Creep stage. A spermatophore is extruded from the male's cloaca onto the ground. After having walked for another several centimeters the male deposits the next spermatophore. By repeating this behavior the male usually deposits two to four spermatophores.

VIII. (Female 4) Sperm pick-up. The female moves over the deposited spermatophore and attempts to stick it onto her cloaca. Not all spermatophores are successfully picked up by the female.

Results

We observed a total of 119 encounters, and the observations of these encounters are summarized in Fig. 1. Based on these observations, we concluded that there are at least four stages during which a female could choose a male: the Approach, Fan, Creep or Spermatophore deposition stages. At any of these stages, females were able to move away from the male.

We noted no conspicuous variations in the Approach, Creep or Spermatophore deposition stages but were able to discriminate four sub-patterns in the male's Fan behavior (Fig. 2). These four fanning sub-patterns were defined as: (A) side-on fanning directly in front of the female ($n = 47$); (B) head-on fanning directly in front of the female ($n = 7$); (C) side-on fanning but off to one side of the female ($n = 5$); (D) fanning that could not be observed by the female ($n = 8$). A significantly higher proportion of male newts displayed sub-pattern (A) Fan behavior than the other sub-patterns (binomial test $n = 67$; $p < 0.001$).

We calculated the correlation coefficients between the morphological characters (SVL, TL, TH, W) and found significant partial correlations between SVL and W ($n = 74$, $r = 0.57$; $p < 0.01$) and between TH and W ($n = 74$, $r = 0.85$; $p < 0.001$; see also Table 1).

Female acceptance

Multiple logistic regression analysis with a backward stepwise mode was applied to test the relationship between a male's Fan display (Fan behavior A vs. no Fan behavior

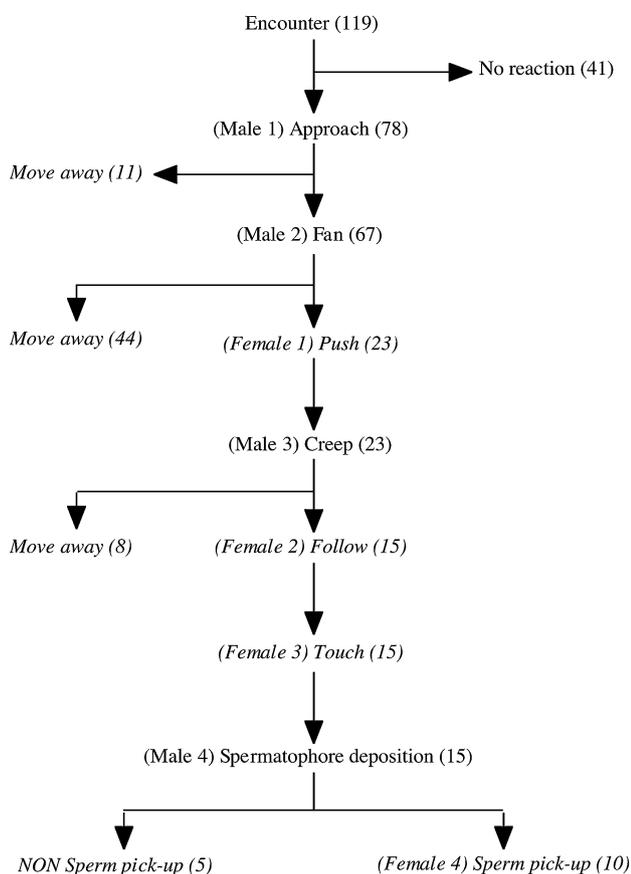


Fig. 1 Flow diagram of sequence of the sexual behavior in the newt *Cynops pyrrhogaster*. *Italics* Actions displayed by female newts, *numbers in parenthesis* observed frequencies

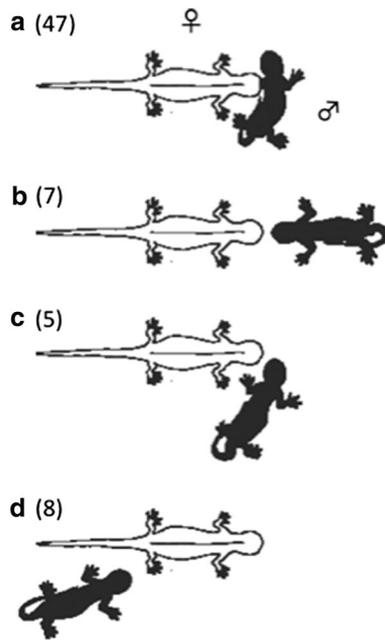


Fig. 2 Observed sub-patterns of the male newt's Fan display. **a** Side-on fanning directly in front of female, **b** head-on fanning directly in front of female, **c** side-on fanning but off to one side of female, **d** fanning that could not be observed by female. Numbers in parenthesis Observed frequencies, black/white representations males/females, respectively

Table 1 Partial correlation coefficients among snout–vent length, tail length, tail height and body mass of the male newt *Cynops pyrrhogaster*

	SVL	TL	TH	W
SVL	–	0.29	–0.21	0.57**
TL		–	0.009	0.05
TH			–	0.85**
W				–

** $p < 0.01$

SVL Snout–vent length, TL tail length, TH tail height, W body mass

A), its morphological characters (SVL, TL and TH) and the breeding season (spring or fall) with the probability of female acceptance at each stage of courtship. To investigate whether the male's Fan display and its morphological characters act independently or not, we added interaction terms to the multiple logistic regression using dummy values to encode the dependent variable (reject: 0, accept: 1), breeding season (spring: 0, fall: 1) and Fan display (no Fan behavior A: 0, Fan behavior A: 1). In the Approach and Spermatophore deposition stages, no variable was significantly associated to the differences in the female's decision. However, from the Fan stage to the Creep stage, TH had a positive effect on the acceptance rate, and SVL and the interaction between mode of the male's fanning

display and SVL were negatively correlated with the female's acceptance rate ($n = 63$, $df = 1$; SVL: estimate = -0.41 , $\chi^2 = 7.68$, $p = 0.006$; TH: estimate = 1.49 , $\chi^2 = 8.39$, $p = 0.004$; Fan display \times SVL: estimate = -0.04 , $\chi^2 = 5.18$, $p = 0.02$; season: estimate = -2.09 , $\chi^2 = 4.60$, $p = 0.03$). Most of the accepted males (20/23) showed the Fan display A pattern in the Fan stage. In the Creep stage, the difference among accepted males and rejected males was marginally significant ($n = 22$, $df = 1$; TH: estimate = 1.04 , $\chi^2 = 3.71$, $p = 0.05$).

Male condition

The relationship between male weight and acceptance by females in the Fan stage was also assessed. To control for the effects of size, we used SVL as the covariate in an analysis of covariance (ANCOVA). The analysis showed that accepted males were significantly heavier than rejected males (ANCOVA, $F_{1, 60} = 123.11$, $p < 0.0001$). In addition, the weight:size ratio differed among males showing different Fan displays (ANCOVA, $F_{1, 58} = 105.25$, $p < 0.0001$): males displaying Fan behavior A were significantly heavier than males showing the other Fan behaviors (ANCOVA, $F_{1, 60} = 110.64$, $p < 0.0001$).

Discussion

Our observations of the courtship behavior of male and female *C. pyrrhogaster* belonging to the Hamakanaya population revealed that (1) females could decide during at least four different stages of a sequential courtship process whether to accept a male or not, i.e. at the Approach, Fan, Creep and Spermatophore deposition stages (Fig. 1); (2) the male newt displayed four sub-patterns of Fan behavior (Fig. 2). Multiple logistic regression analysis of the Fan stage revealed that accepted males had relatively small SVL and high TH values and that females evaluated the mode of Fan display in combination with SVL; in the Creep stage, males with relatively high TH values were preferred.

Most of the accepted males (20/23) showed fanning sub-pattern A (side-on fanning directly in front of the female, $n = 47$) in the Fan stage, suggesting that females tend to accept males with Fan display A, smaller SVL and higher TH in the Fan stage. It is therefore possible that a male newt may increase its appeal to females by displaying fanning sub-pattern A. Any one female newt is courted by many males simultaneously, therefore attracting the attention of a female newt is crucial for the success of males in this species. However, if Fan display A is advantageous, then why do some males perform other less advantageous

displays? One possible explanation is the specific Fan display also indicates the condition of the male.

The result of the ANCOVA shows that relative weight differed among males showing different Fan displays. Hence, it is possible that body condition may dictate the Fan display, with only males in better condition able to prefer in Fan display A; however, further research is needed for a definitive conclusion to be drawn. In *C. pyrrhogaster*, females are attracted by the male pheromone, “Sodefrin” (Kikuyama et al. 1995). This pheromone is species specific based on experiments showing that it does not attract females of *C. ensicauda*, a closely related newt species (Kikuyama et al. 1995). Hence Sodefrin may potentially be used by females as a signal for species recognition during mating. In males with high TH, the Fan display may serve to create a stronger water flow towards the female compared to that created by low TH males, and thus the former may be preferred by females.

Males may be able to transmit Sodefrin to females more efficiently using fanning sub-pattern A than by using the other Fan sub-patterns. Treer et al. (2013) showed that male pheromones are emitted to the approached female during the fanning behavior. However, additional experiments are needed to test this hypothesis.

In a rough-skinned newt (*Taricha granulose*), males experience strong sexual selection based on TH and large body size (Jones et al. 2002). In our study, however, accepted males were smaller than rejected males, although they were heavier relative to structural size than rejected males when SVL was controlled for. Body size is a sexually dimorphic trait in *C. pyrrhogaster*, with females being smaller than males (Sawada 1963a). Since fatness is an indicator of body condition (Sargent et al. 1998), females might prefer males in good condition. The observed trend can be explained by smaller males tending to be in good condition. However, more studies are required to establish the cause of the observed trends.

Newts of the genus *Triturus* show sexual dimorphism in tail characteristics (Halliday 1977; Malmgren and Thollesson 1999). Only males have dorsal crests, which begin just behind the head and extend backwards as a vertical tail extension. Several studies have shown that the tail sizes or crest heights of males in this genus are associated with the number of spermatophores accepted by females (Malacarne and Cortassa 1983; Green 1991; Gabor and Halliday 1997). There is additional evidence that crest height in *T. vulgaris* is related to the body condition of individuals (Baker 1992). By experimental manipulation of food levels, Green (1991) found that TH decreased more rapidly in starved individuals than in fed ones, leading to the suggestion that *Triturus* females choose males with good condition using the dorsal crest as an indicator. In *C. pyrrhogaster*, females accepted males with relatively high

tails. We found the TH height strongly correlated with body mass. Therefore, it is possible that *C. pyrrhogaster* females choose males with a good condition using TH as an indicator, as in *Triturus*. Experiments which manipulate body condition are needed to test this hypothesis.

Another possibility is that TH is correlated positively with the efficiency of sending male pheromones to the approached females. Thus, if a high TH can send the Sodefrin (Kikuyama et al. 1995) to the approached female more efficiently, males with high TH are likely to be accepted by females. The observed female preference to higher TH may be a mere correlation and thus not the causation. Additional experiments are needed to test this hypothesis.

Nuptial color was not tested in our study. However, Secondi et al. (2012) reported that under UV light, the nuptial color of *Lissotriton vulgaris* is more attractive to females. Further experiments to elucidate the role of the nuptial color in *C. pyrrhogaster* are required.

The observations reported here show that *C. pyrrhogaster* females in the Hamakanaya population accept males with both specific courtship behavior and morphological characters. In addition, we found that females preferred males that show Fan display sub-pattern A combined with SVL. These results suggest that female newts choose males during the Fan stage using both behavioral and morphological characters (or related olfactory characters; see the above discussion), but use only morphological characters during the Creep stage. For example, in the males of sage grouse *Centrocercus urophasianus*, the inter-pop interval (the interval between the two popping notes that terminate the strut display) affects whether a female sage grouse visits a male, but it has no effect on female mate-choice once the visit has begun (Gibson 1996). Conversely, another male trait, the display rate, does not affect whether a female visits a male, but it does affect whether the female mates with the male during a visit. In the newt *C. pyrrhogaster*, females may choose their mates in a stepwise or graded manner, i.e. the females first choose a male's Fan display, then choose its morphological characters. Another possibility to explain female preference for a specific Fan display and for certain morphological characters is that both Fan display and the morphological characters have an effect on transmitting the pheromone efficiently. Further research will determine whether these traits act in combination or are independent of each other.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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