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Source: Zoological Science, 25(4) : 355-363

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zsj.25.355>

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# Morphological Asymmetry of the Abdomen and Behavioral Laterality in Atyid Shrimps

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Morphological asymmetry and behavioral laterality in vertebrate species have been intensively studied in recent years, while comparable invertebrate studies are rare. Here we demonstrate asymmetry in the curvature of the abdomen and laterality in evasive responses for two atyid shrimps, *Limnocaridina latipes* and *Neocaridina denticulata*. The frequency distributions of the angle of the abdominal curvature in both species were discretely bimodal, suggesting that the two populations are composed of both left- and right-type individuals. In *N. denticulata*, behavioral analysis using high-speed filming illustrated that the escape direction for each individual, evoked by a sudden non-lateralized stimulus, was correlated with its abdominal curvature: left- (right-) type shrimp jumped back-leftward (-rightward) significantly more than often. A crossing experiment with *N. denticulata* indicated that the trait frequency in the F1 generation from two left-type parents differed significantly from that of the F1 generation from two right-type parents, and that the trait frequency for the F1 generation from parents of different laterality types did not deviate from random. That is, offspring laterality type is affected by the lateralities of the parents, indicating that abdominal dimorphism in shrimp is genetically derived. These results suggest that shrimp have an innate laterality that controls their escape direction, which in turn may affect prey-predator interactions in the aquatic community.

**Key words:** abdominal curvature, antisymmetry, behavioral laterality, decapod, escape response, genetic basis, *Neocaridina denticulata*, morphological asymmetry, *Limnocaridina latipes*, tail-flip

## INTRODUCTION

Many vertebrate taxa show elaborate asymmetry along the left-right axis (e.g., Vallortigara and Rogers, 2005). Particularly, morphological asymmetry in the mouth of Tanganyikan scale-eating cichlid fishes provides a typical example of antisymmetry (Liem and Stewart, 1976; Hori, 1991, 1993). In these fishes, the mouth opens either leftward (termed 'righty' by Nakajima et al. [2004], since the right side of the head faces somewhat frontward) or rightward ('lefty'), due to an asymmetrical joint of the lower jaw to the suspensorium (Liem and Stewart, 1976; Hori, 1991, 1993). The morphological asymmetry provides an advantage when the individual tears off scales from prey fish (Hori, 1993). Similar mouth dimorphisms have been found in other fishes (Mboko et al., 1998; Seki et al., 2000; Hori et al., 2007; Nakajima et al., 2007; Takeuchi and Hori, 2008). When largemouth bass, *Micropterus salmoides*, were angled in an artificial pond, lefties and righties were hooked on the left and right side of their mouths, respectively (Nakajima et al., 2007). Investigations of parental and offspring mouth morphologies for several fishes (scale-eating cichlid [Hori, 1993; Hori et al., 2007], algae-eating cichlid [Hori et al., 2007], freshwater goby [Seki et al., 2000]) indi-

cated that mouth laterality was genetically determined following a Mendelian one locus-two allele system, with the lefty dominant over the righty.

Recently, we found that the shrimp-eating cichlid *Neolamprologus fasciatus* in Lake Tanganyika also showed mouth laterality (Takeuchi and Hori, 2008). The mouth laterality in this fish correlated with behavioral laterality during hunting: when aiming at prey, lefties (righties) frequently bent the right (left) side of their body, abutting a rock. It was suggested that when the hunting strategy corresponded to an individual's mouth laterality (i.e., rightward hunting by lefties and leftward hunting by righties), higher hunting success on shrimp was achieved than for reverse hunts. Through mathematical simulations, Nakajima et al. (2004) showed that the persistence of predator dimorphisms requires the presence of prey dimorphisms and a close relationship between predation success and the predator and prey dimorphisms. Therefore, the shrimp *Limnocaridina latipes*, which is hunted by several shrimp-eating cichlids including *N. fasciatus* (Yuma et al., 1998), is considered to have laterality in its escape response.

In invertebrate species, few studies have focused on behavioral lateralities in evasion. However, many researchers have reported a mechanism of escape behavior for crustaceans. When lobsters and shrimp react to approaching predators or other threats, they produce a series of rapid swimming movements called 'tail-flips' (lobster [Chapman and Rice, 1971], crayfish [Wine and Krasne, 1972; Wine,

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doi:10.2108/zsj.25.355

1984], brown shrimp [Arnott et al., 1999]). The tail-flip consists of a sequence of flexion and extension of the abdomen, which then propels the individual backwards through the water (Newland and Neil, 1987). During the tail-flip, shrimp are able to exert some control over their swimming direction. The greatest steering effect is produced by lateral rotation of the abdomen against the carapace: leftward abdominal rotation results in movement backward and to the left, and rightward rotation produces movement backward and to the right (Newland et al., 1992). If the abdomen is curved to either side, and the curvature is an innate character, this morphological asymmetry should affect an individual's escaping direction.

Here we demonstrate laterality in two atyid shrimps, *Limnocaridina latipes* and *Neocaridina denticulata*, by showing (1) abdominal curvature to either side, with the curvature frequency showing a discrete bimodal distribution, (2) linkage between escape direction and abdominal curvature, and (3) a genetic basis for abdominal curvature.

## MATERIALS AND METHODS

### Study organisms

Morphological measurements of abdomen asymmetry were conducted on *Limnocaridina latipes* Calman, a relatively small atyid shrimp (maximum body length, 9 mm) endemic to Lake Tanganyika. Samples were collected using SCUBA gear and hand nets (5–10 m water depth) at Kasenga Point (8°43'S, 31°08'E) near Mpulungu, Zambia, at the southern end of the lake in September 2006. The samples were kept in individual 1.5-ml tubes filled with 10% formalin. Body lengths were determined by measuring the distance from

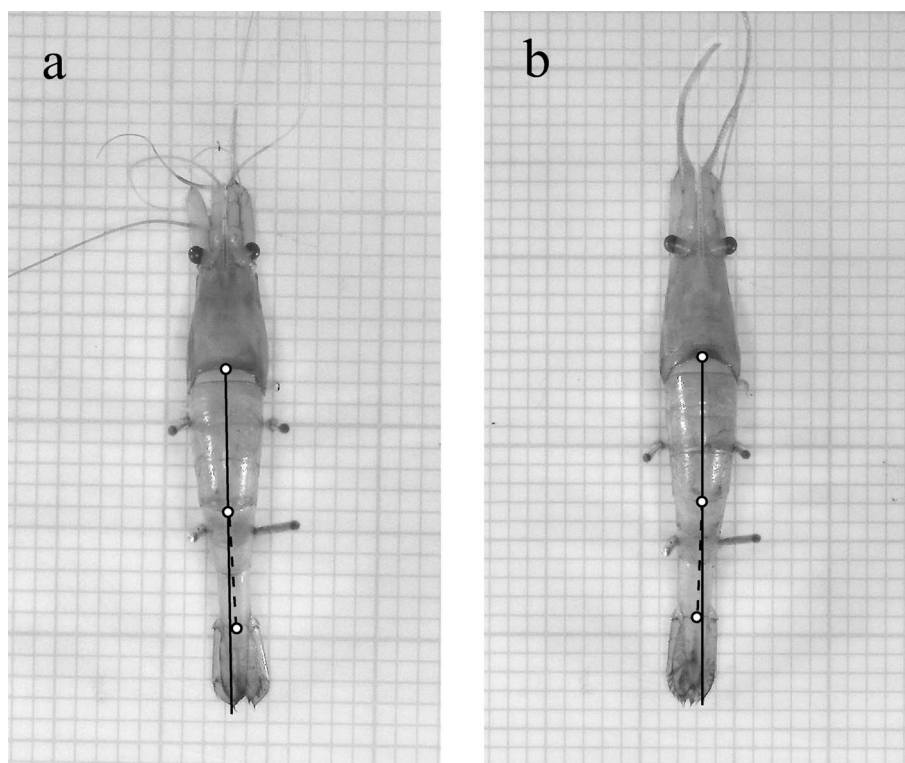
the base of the rostrum to the posterior edge of the telson.

As *L. latipes* was difficult to raise and identify to sex, investigations on escape response and crossing experiments were instead conducted on the Japanese atyid shrimp *Neocaridina denticulata* De Haan. In rivers and ponds, *N. denticulata* is consumed by carnivorous or omnivorous fishes, such as the largemouth bass, *Micropterus salmoides* (Azuma and Motomura 1998). Largemouth bass show left-right differences in mouth morphology and behavior (Nakajima et al., 2007; Yasugi and Hori, unpublished data). Individuals of *N. denticulata* were collected using hand nets from the Kamogawa River (35°15'N, 135°46'E) in June 2007 and Mizorogaike Pond (35°03'N, 135°50'E) in May 2004; both locations are in Kyoto, Japan. The shrimp from the Kamogawa River were analyzed for abdominal morphology and used for escape response analysis. The shrimp from Mizorogaike pond were used in a crossing experiment. The shape of the appendix masculine was used to identify the sex of *N. denticulata* individuals.

The shrimp used for morphological analysis were narcotized with 0.003% eugenol and kept in individual 1.5-ml tubes filled with 70% ethanol. To preserve the natural curvature of the abdomen, shrimp were always placed head down in the tubes.

### Morphological measurement of abdominal curvature

To quantify the abdominal curvature, the carapace was placed horizontally and the angle between the fore and hind halves of the abdomen was measured as follows. The dorsal sagittal-lines of the fore half and the hind half of abdomen were defined based on the dorsal abdominal artery and hindgut: the former is the line from the center of the posterior edge of the carapace to the center of the third abdominal segment, and the latter is the line from the center of the posterior edge of the third abdominal segment to the center of the sixth abdominal segment (Fig. 1). The angle was designated



**Fig. 1.** Photographs illustrating abdominal curvature of the left-type (**a**) and right-type (**b**) in *Neocaridina denticulata*. The abdominal curvature angle is measured from the intersection of two dorsal sagittal lines: one (solid line) runs from the posterior edge of the carapace to that of the third abdominal segment, and the other (dashed line) from the third abdominal segment to the sixth. The grid size of the underlying section paper is 1×1 mm. The abdominal laterality of *Limnocaridina latipes* was defined in the same way.

as the abdominal curvature angle ( $\alpha$ ) and was measured using a digital microscope with image analysis software (VHX-100, Keyence, Osaka, Japan) with an accuracy of  $0.07^\circ$ . Measurements were taken three times for each shrimp, with the shrimp being repositioned on the microscope stage each time. Since measuring the angle of a three-dimensional object is prone to yield some extreme values, median values were used for the following analysis instead of mean values (in actuality, the measurement errors were small [ANOVA: *L. latipes*,  $F_{326}=578.7$ ,  $P<0.001$ ; *N. denticulata*,  $F_{314}=187.5$ ,  $P<0.001$ ]). Positive values were assigned to abdomens that curved to the left side, while negative values were given to abdomens that curved to the right. Shrimp with  $\alpha<0$  were designated as 'left-types' (Fig. 1a), and those with  $\alpha>0$  as 'right-types' (Fig. 1b). This type assignment was designed to accord with the mouth laterality of fish (Nakajima et al., 2004).

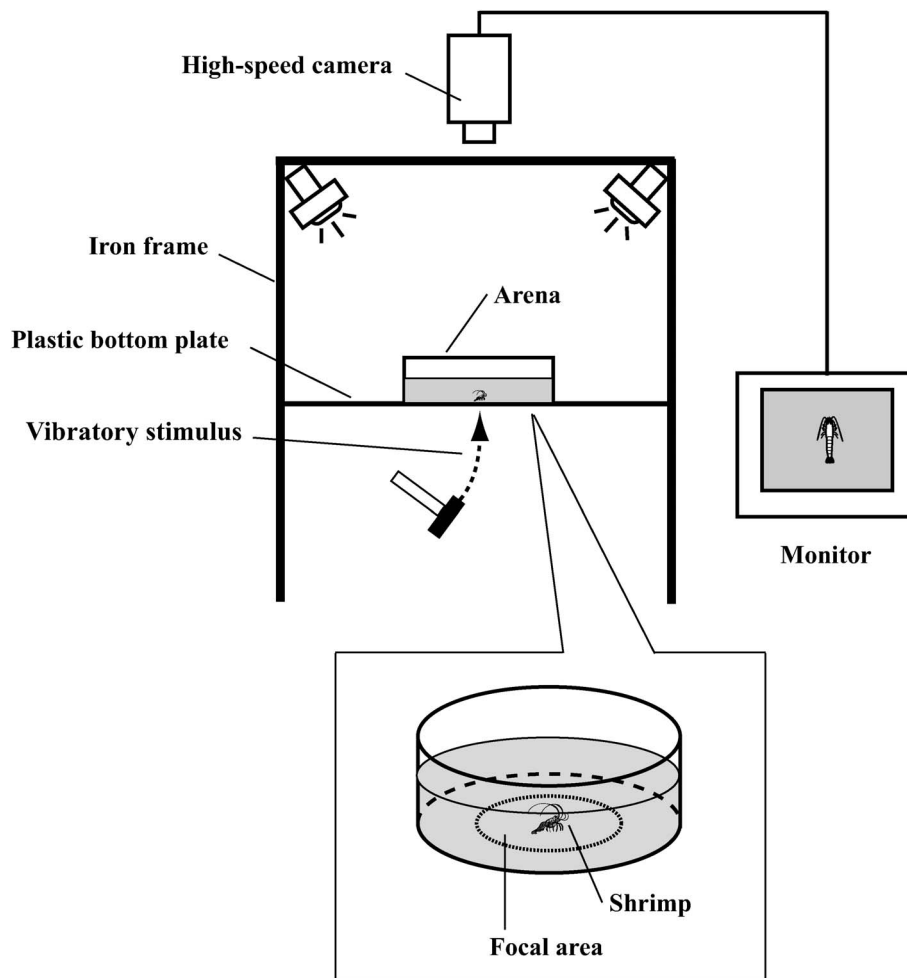
#### Analysis of escape response

The directions in which *N. denticulata* individuals attempted to escape when exposed to a vibratory stimulus was tested in the laboratory. Directional stimuli (e.g., direct contact or visual stimulus) may not be appropriate for tests of lateral biases in behavior since the subjects appear to perceive the direction of the stimulus. Therefore, vibratory stimuli are commonly used to evoke escape responses in fish (e.g., Heuts, 1999).

The test was conducted using a large petri dish 'arena' (diam-

eter 25 cm, water depth 2 cm) that was placed on a section paper and surrounded by a black screen (Fig. 2). Shrimp escape behaviors were recorded with a high-speed video camera (VCC-H300, Digimo, Osaka, Japan) located above the arena. The video frames were grabbed with a time resolution of 90 frames/s using ImageHyper, and a resolution of  $512\times 512$  pixels. Four lights (100W) were directed toward the arena to provide sufficient illumination for the high-speed video recordings.

Before the test, the shrimp were kept in aquaria for at least 1 day, and for no longer than 2 weeks after collection from the field. None of the shrimp showed obvious signs of poor health or damage. During each trial, one shrimp was settled at the center of the arena and enclosed within an opaque plastic cylinder (diameter 9.5 cm, height 10 cm) for 7 min. The cylinder was then gently removed. The plastic bottom plate that supported the arena was then struck with a hammer from behind to evoke an escape response. All hammer strikes were landed at just behind the arena center, which was not visible to the shrimp. One trial was conducted for each shrimp, and only the first tail-flip was used for analysis. To avoid any confounding effects from the arena walls, only responses that did not pass outside a 'focal area' (a circle of diameter 16 cm at the center of arena) were analyzed. If the shrimp swam out of the focal area before stimulation or failed to respond to the stimulus, the trial was terminated and the shrimp was removed from the arena. In most cases, the shrimp made a swift jump backwards, either to the left



**Fig. 2.** Schematic diagram of the apparatus for observation of shrimp escape responses. Shrimp in the arena were stimulated with vibrations by striking the plastic bottom plate with a hammer from behind.

or the right within the focal area. Six trials were excluded from the analysis because the shrimp jumped almost upward with no clear horizontal direction.

The jumping angle of each shrimp was defined as the angle between two lines, namely, its original body axis and stretch toward the arrival point. Specifically, the former was defined as the line from the midpoint between the eyes to the posterior edge of the sixth abdominal segment just before jumping, and the latter was defined as a line from the midpoint of the eyes before jumping to the midpoint of the eyes after the first tail-flip. Jumping angles between  $0^\circ$  (jumping just behind) and  $180^\circ$  (just in front) on the right side of the shrimp were assigned positive values, and those between  $0^\circ$  and  $180^\circ$  on the left side were assigned negative values. A total of 64 trials (body length mean $\pm$ SD,  $22.2\pm 2.1$  mm; body height, 4.0–6.0 mm; males=32, females=32) were used for statistical analyses.

After observation of the escape response, the abdominal curvature angle of the shrimp was measured using the method described above. The measurements were taken without reference to the escape behavior data. The relationship between escape direction and abdominal laterality was analyzed using a chi-squared test for contingency tables. The distribution of jumping angles was tested for deviations from a unimodal distribution (von Mises distribution) using Watson's test. In addition, the jumping speed of the first tail-flip was calculated using the digitized position data to examine whether there was a left-right difference in jumping speed for each laterality type.

#### Crossing experiment

The laterality type of live or fresh shrimp is currently difficult to determine. In crossing experiments, therefore, the parental shrimp were paired randomly, and their laterality types were examined by fixation after all breeding was completed. The crossing experiment was designed to use three replicates with four combinations of parental laterality types: left type  $\times$  left type (L $\times$ L), left type (male)  $\times$  right type (female) (L $\sigma$  $\times$ R $\phi$ ), right type (male)  $\times$  left type (female) (R $\sigma$  $\times$ L $\phi$ ), and right type  $\times$  right type (R $\times$ R). To produce these replicates, the obtained broods were first separated into four combinations of parental laterality types. Next, the three most successful broods, in respect to the number of offspring, were selected as replicates from each combination and the laterality type of every offspring was determined.

The laboratory was kept at  $22\text{--}23^\circ\text{C}$  under a 14L:10D regime. We considered that there is no possibility that stored sperm is used for fertilization because caridean shrimps do not possess any sperm storage structures (Bauer, 1976; Bauer and Holt, 1998). To avoid copulation before the experiment, males and females were kept separately in plastic containers (20 $\times$ 12 $\times$ 13 cm) for at least 2 weeks in the laboratory, and females that held eggs after being separated from males were excluded from the experiment. The shrimp did not spawn later than several days after separation. Thereafter, one male and one female were placed in a small plastic container (15 $\times$ 9 $\times$ 11 cm) for breeding. As atyid shrimp have direct development after the egg stage, young shrimp (1 mm in body length) start swimming by themselves about 20 days after coupling. The shrimp were fed fish pellets (Tetra Plankton, Tetra Japan, Tokyo, Japan).

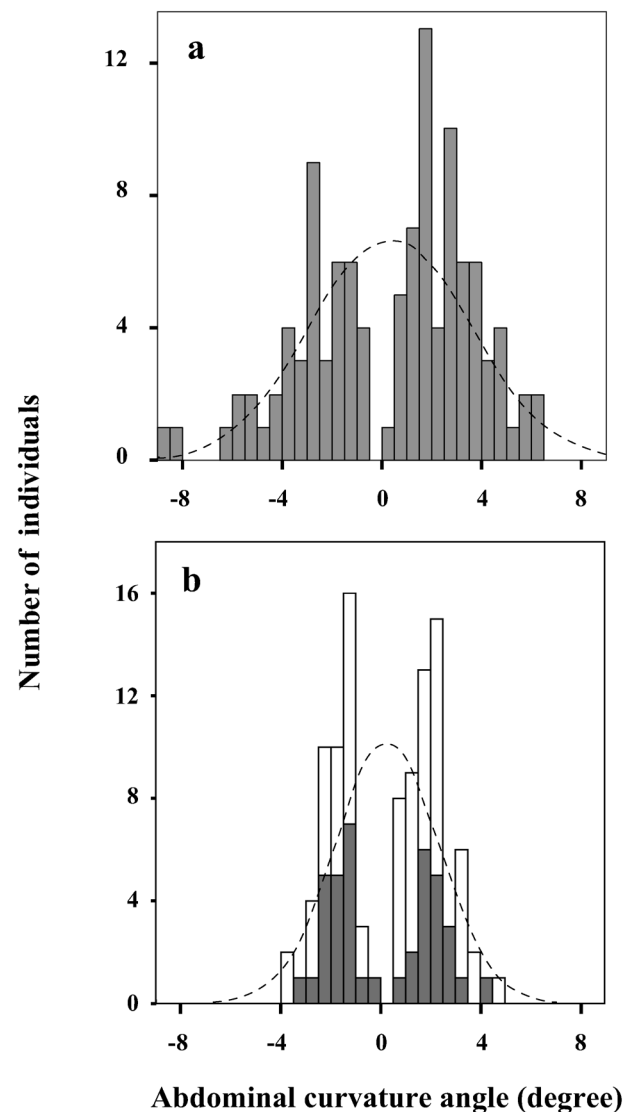
After achieving sufficient development (more than 1 cm in body length), young shrimp were narcotized and kept as described above. In total, 508 young shrimp (body length,  $13.82\pm 3.02$  mm) were obtained from 12 pairings, and their abdominal curvatures were measured as described above. If abdominal laterality has no genetic background, we would predict that the frequencies of offspring laterality types would have no relation to the parental types. A Watson's test was performed using the R statistical package. Other statistical analyses were performed using JMP version 5 (SAS Institute, Inc.).

## RESULTS

### Morphological asymmetry of abdominal curvature in two shrimp species

The abdomens of *L. latipes* (body length, mean $\pm$ SD:  $4.78\pm 0.62$  mm) curved either leftward ( $2.72\pm 1.48^\circ$ ,  $n=64$ ) or rightward ( $-2.93\pm 1.88^\circ$ ,  $n=45$ ) (Fig. 3a). Only one shrimp showed a small curvature of the abdomen ( $-0.5^\circ < \alpha < 0.5^\circ$ ). The frequency distribution of abdominal curvature was clearly bimodal and differed significantly from normal (Shapiro-Wilk test:  $W=0.956$ ,  $P=0.007$ ).

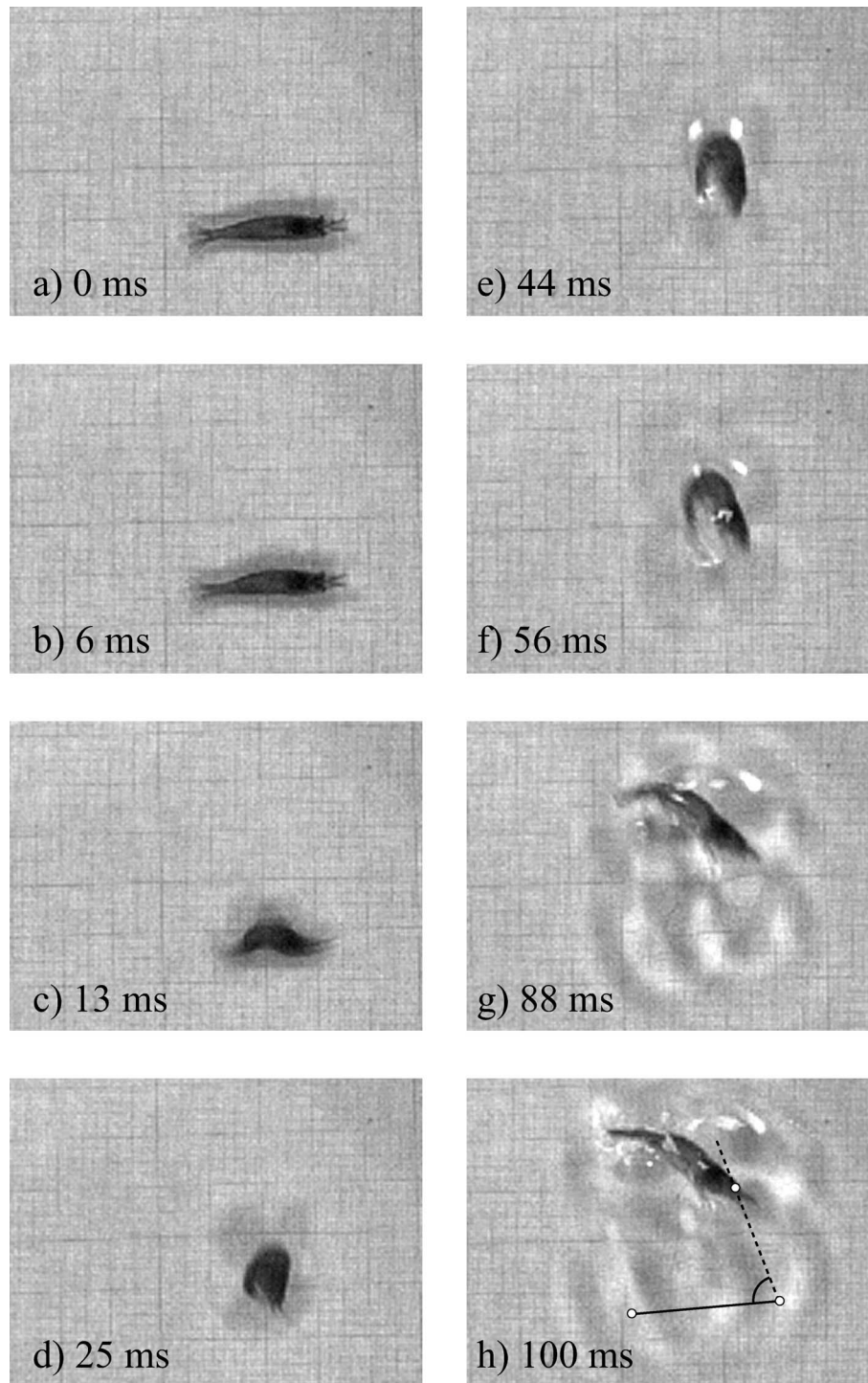
The abdomens of *N. denticulata* (body length,  $22.17\pm 0.62$  mm) also curved either leftward ( $2.04\pm 0.92^\circ$ ,  $n=58$ ) or rightward ( $-1.80\pm 0.74^\circ$ ,  $n=47$ ) (Fig. 3b). The fre-



**Fig. 3.** Frequency distribution of the abdominal curvature angle of *L. latipes* (a) and *N. denticulata* (b) in each natural population. The dashed line indicates the normal curve fitted to the data. In *N. denticulata*, the dark column indicates males and the open column indicates females. The sexes of *L. latipes* individuals could not be determined.

quency distribution of their abdominal curvature was again clearly bimodal and differed significantly from normal (Shapiro-Wilk test:  $W=0.922$ ,  $P<0.001$ ). The dimorphism

was shown in both sexes, and no significant difference between sexes was detected in the frequency of laterality type (likelihood ratio test:  $\chi^2=1.56$ ,  $P=0.211$ ).



**Fig. 4.** Sequence of 'tail-flip' escape responses (a leftward jump in this case) of *N. denticulata* evoked by vibrations: **(a)** just after vibration (0 ms), **(b)** abdomen rotating leftward, **(c)** the body lying to left side and the abdomen flexing, **(d)** the body starting to move back and to the left, **(e)** flexion of the abdomen completed, **(f)** extension of the abdomen starting, **(g)** abdomen extending, and **(h)** the first tail-flip completed and movement of the body stopped. The jumping angle was defined as the angle between two lines: one (solid line) from the midpoint between the eyes to the posterior edge of the sixth abdominal segment just before jumping, and the other (dashed line) from the midpoint of the eyes before jumping to the midpoint of the eyes after the first tail-flip. The grid size of the underlying section paper is 1×1 mm. The video image was filmed from a fixed point at a frame rate of 160 frames/s.

Escape response evoked by vibratory perturbation

Each shrimp performed tail-flips 1 to 5 times within the focal area after the vibratory stimulus. The detailed sequence of evasive movements elucidated from the test was as follows. First, the abdomen was rotated laterally against the anterior-posterior axis, causing the shrimp to move in a horizontal direction (Fig. 4). Next, the uropods were thrust by tight flexion of the posterior abdomen, providing propulsion. Finally, the shrimp changed the escape pathway in the horizontal plane through successive tail-flips.

The shrimp jumped either back and to the left or back and to the right, but never simply backward or forward. Since no significant difference was observed in the tendency of jumping angle between the sexes, the data from both sexes were pooled. The frequency distribution of jumping angles was bimodal and differed significantly from a von Mises distribution for each laterality type (Fig. 5; Watson’s test: left type,  $P<0.01$ ; right type,  $P<0.01$ ). The distributions of left types and right types showed the highest peak around  $-60^\circ$  and  $60^\circ$ , respectively.

From the morphological measurements, the 64 shrimp used in the escape response analysis included 34 left-type and 30 right-type individuals. Although shrimp of either laterality type jumped to both sides, left-type shrimp jumped back and to the left (leftward jump) more frequently than they jumped back and to the right (rightward jump), with the

reverse being true for right-type individuals. Abdominal laterality was significantly related to escape direction (Table 1;  $\chi^2=12.52$ ,  $P<0.001$ ). However, we found no significant correlation between the magnitude of the abdominal curvature angle and that of the jumping angle (leftward jumps of left types,  $F_{2,4}=1.12$ ,  $P=0.302$ ; rightward jumps of right types,  $F_{2,0}=0.04$ ,  $P=0.844$ ).

**Table 1.** Number of *N. denticulata* individuals showing leftward jumps and rightward jumps in response to vibration, for two laterality types.

Abdominal laterality	Escape response	
	Leftward jump	Rightward jump
Left-type	25	9
Right-type	9	21

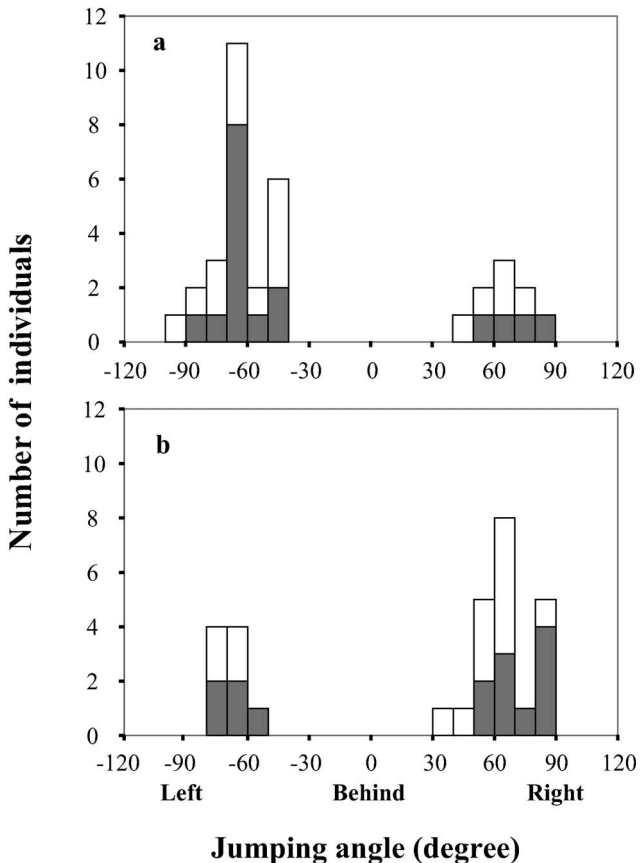
The jumping speed (mean $\pm$ SD) of the first tail-flip was  $0.31\pm0.11\text{ m s}^{-1}$ . There was no difference in jumping speed between laterality types (Student’s  $t$ -test:  $t=1.48$ ,  $P=0.145$ ). In both types, the speed of leftward jumps did not significantly differ from that of rightward jumps (Wilcoxon signed rank test: left type,  $z=-0.23$ ,  $P=0.815$ ; right type,  $z=-1.04$ ,  $P=0.298$ ).

Inheritance patterns of abdominal laterality

The results of the crossing experiment are summarized in Table 2. The frequency distribution of abdominal curvature angles of the F1 generation had two peaks, and no symmetrical individuals appeared in any crossing type (Fig. 6). Within each crossing type, the pattern of F1 frequencies was not significantly different between broods (chi-squared test: L $\times$ L,  $\chi^2=0.049$ ,  $P=0.976$ ; L $\times$ R,  $\chi^2=1.136$ ,  $P=0.567$ ; R $\times$ L,  $\chi^2=0.447$ ,  $P=0.799$ ; R $\times$ R,  $\chi^2=0.425$ ,  $P=0.809$ ). Between crossing types, on the other hand, L $\times$ L parents always produced more left- than right-type offspring, and R $\times$ R parents produced the opposite trend. L $\sigma \times$  R $\phi$  parents and R $\sigma \times$  L $\phi$  parents always produced similar numbers of left- and right-type offspring. The frequency of laterality types in the F1 generation was significantly correlated with the crossing type of the parents (GLM:  $\chi^2=20.39$ ,  $P<0.001$ ). The F1 frequencies from L $\times$ L parents significantly differed from those produced by R $\times$ R parents (Table 3). Thus, the laterality types of the parents were considered to affect those of the offspring.

DISCUSSION

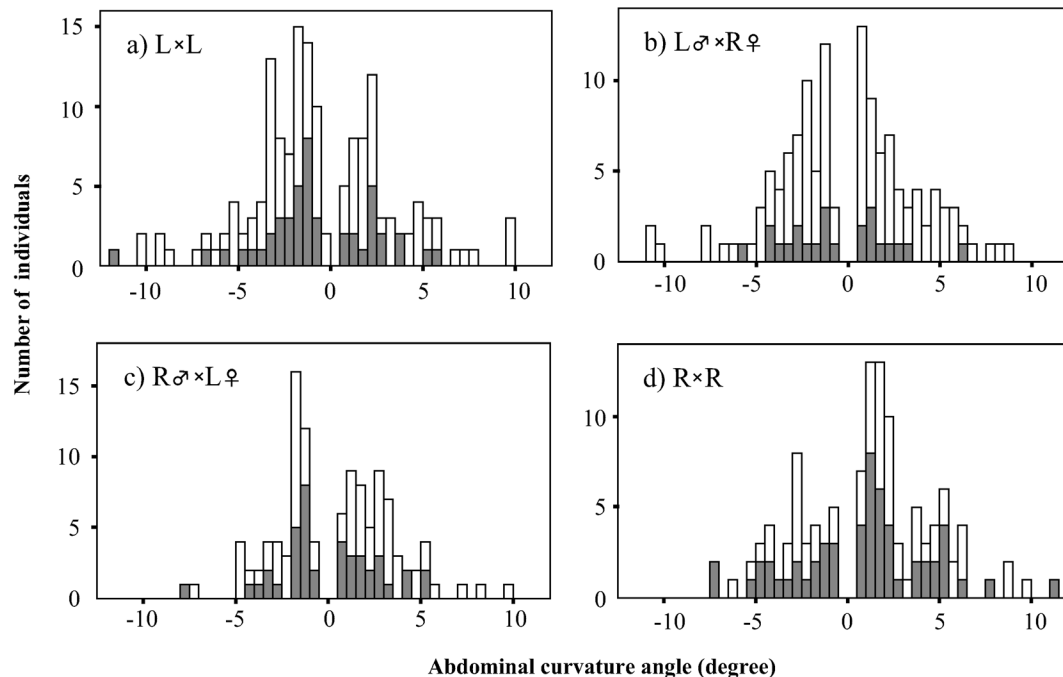
The results of the morphological measurements demonstrated that the populations of *L. latipes* and *N. denticulata* were composed of left-type and right-type individuals with respect to abdominal curvature. This type of morphological asymmetry is categorized as antisymmetry, rather than as fluctuating asymmetry or directional asymmetry (Palmer and Strobeck, 1986). The pattern of bimodal distribution found in the abdominal curvature of these shrimp was consistent with the distribution of left-right differences found in the mouth asymmetries of several fishes (Hori, 1993; Mboko et al., 1998; Seki et al., 2000; Hori et al., 2007; Nakajima et al.,



**Fig. 5.** Frequency distribution of jumping angle in left-types (a) and right-types (b) of *N. denticulata*. Dark and open columns indicate males and females, respectively.

**Table 2.** Results of crossing experiments on *N. denticulata*. SR, segregation ratio.

Mating	Number of offspring			Abdominal curvature angle (degree)		Abdominal laterality		
	Total	Male	Female	Left-type	Right-type	Left-type	Right-type	% Left-type
<b>L×L</b>								
1	52	22	30	-2.77±1.91	3.29±2.38	32	20	61.5
2	35	19	16	-3.02±2.72	2.93±2.42	22	13	62.9
3	66	5	61	-3.31±2.54	3.41±2.34	40	26	60.6
Total	153	46	107			94	59	
SR						1.59	1.0	
<b>L♂×R♀</b>								
1	33	19	14	-3.43±2.99	3.09±2.46	18	15	54.5
2	68	0	68	-3.08±2.41	3.30±2.14	31	37	45.6
3	27	4	23	-3.36±1.02	1.58±0.44	15	12	55.6
Total	128	23	105			64	64	
SR						1.0	1.0	
<b>R♂×L♀</b>								
1	30	16	14	-1.54±0.71	2.15±1.06	14	16	46.7
2	41	7	34	-2.95±2.06	3.50±2.27	18	23	43.9
3	41	20	21	-2.55±1.19	2.75±1.75	21	20	51.2
Total	112	43	69			53	59	
SR						1.0	1.15	
<b>R×R</b>								
1	31	8	23	-3.05±1.68	4.29±2.95	11	20	35.5
2	43	22	21	-2.13±1.09	3.30±2.22	13	30	30.2
3	41	26	15	-3.92±1.87	2.28±1.44	15	26	36.6
Total	115	56	59			39	76	
SR						1.0	1.95	

**Fig. 6.** Frequency distribution of abdominal curvature angle for the F1 generation from a crossing experiment in *N. denticulata*. Results are shown for each combination of parent laterality types. Dark and open columns indicate male and female offspring, respectively.**Table 3.** Results of GLM analysis on phenotype frequencies in the F1 generation of *N. denticulata* resulting from the parental phenotypes. R×R pairs were defined as the criterion for comparison.

Variable	Coefficient	SE	$\chi^2$	P
L×L	-0.543	0.149	13.32	<0.001
L♂×R♀	-0.077	0.155	0.25	0.618
R♂×L♀	0.030	0.162	0.03	0.853

2007; Takeuchi and Hori, 2008). The lateral mouth dimorphism found in these fishes correlated with behavioral laterality that resulted from some functional lateral difference, such as dominance in locomotion and/or in sensory abilities of one side of the body over the other (Hori, 1993; Seki et al., 2000). The following question therefore arises: does the abdominal laterality of shrimp produce behavioral laterality,



as do mouth lateralities of fish?

The direction of the evasive response caused by a non-lateralized stimulus in *N. denticulata* was significantly related to abdominal laterality: left-type shrimp jumped back and to the left, probably because their abdomen was curved to the right, and right-type shrimp showed the opposite response. This result suggests that shrimp show behavioral laterality in their evasive response. A similar response has been reported in the brown shrimp *Crangon crangon*: it escapes laterally, either rightward or leftward, when startled by a directional stimulus such as an approaching predatory fish or an artificial rod (Arnott et al., 1999). Therefore, even if *N. denticulata* is perturbed by such directional stimuli, it may escape laterally.

If the escape direction of shrimp depends on structural constraints imposed by the abdominal curvature, left-type shrimp should exclusively escape back and to the left while right-type shrimp should escape to the right. However, structural constraints impose an obviously non-adaptive character, since shrimp would be unable to change their escape direction, regardless of the direction from which a predator approached. Our escape response results indicate that left-type and right-type shrimp show low levels of reverse tendency against the escape direction expected from their abdominal curvature (rightward jumps by left-types, 9/34 trials, leftward jumps by right-types, 9/30 trials, Table 1). Shrimp may be able to escape in both directions, regardless of their type. Therefore, although escape direction may be affected by abdomen morphology, because of intra-individual behavioral flexibility, the direction may not be fixed.

The movements of the abdomen during tail-flip have been intensively studied at the neuronal level in crayfish (Wine and Krasne, 1982; Newland and Neil, 1990; reviewed by Edwards et al., 1999). There are two pairs of giant fibers in the ventral nerve cord, the lateral giants (LGs) and the medial giants (MGs), that produce a tail-flip with an upward and with a flat backward trajectory, respectively (Wine, 1984; Krasne and Wine, 1988). LGs respond to stimuli to the abdomen, whereas MGs respond to stimuli to the rostrum or cephalothorax (Wine and Krasne, 1982). In 70 trials of *N. denticulata*, 64 trials used in the analysis were horizontal trajectories, and the remaining six trials that were excluded from the analysis were upward trajectories. If the neuronal basis of the tail-flip in *N. denticulata* is the same as that in crayfish, the former may excite the MGs, while the latter may excite the LGs. Further work is needed to understand in detail the neuronal control of the tail-flip of atyid shrimps.

The results of our crossing experiment suggest that abdominal dimorphism has some genetic basis. However, we could not provide a simple scheme for the genetic system of abdominal laterality, for two reasons. First, parents of the same laterality type produced a certain number of offspring with the opposite laterality type. Thus, we could not determine which laterality type was dominant if we assumed a simple Mendelian inheritance scheme. The genetic system of abdominal laterality in shrimp seems to be different from that of mouth laterality in fish, in which lefties are dominant over righties in a Mendelian inheritance pattern (Hori, 1993; Seki et al., 2000; Hori et al., 2007). Second, the frequency of the abdominal curvature angle showed a discrete bimodal

distribution, i.e., the phenotypic forms of the abdominal curvature were separated into two types with no symmetrical individuals occurring. Therefore, a quantitative genetic model cannot be applied to this case; if a simple quantitative model could account for the abdominal laterality, the frequencies should be consistent with a unimodal distribution. Further studies including backcrosses of the F1 and F2 generations are necessary to determine the genetic system of abdominal laterality.

The mouth laterality of Tanganyikan shrimp-eating cichlid *N. fasciatus* is related to its predation behavior: lefties tend to dash at targeted prey with the right side forward, and righties with the left side forward (Takeuchi and Hori, 2008). Taking into account our finding that the abdominal curving of shrimp is a lateral dimorphism that is related to their escape direction, we can predict that outcomes of predator-prey encounters are affected by both the abdominal laterality in shrimp and the mouth laterality in shrimp-eaters. Predator-prey interactions can be strongly affected by a prey's morphology and behavior (Sih and Moore, 1990). Both the predation and escape success may depend on the interaction of the laterality types between the individual shrimp and fish during an encounter. In fact, Takeuchi and Hori (2008) indicate that predation success in the shrimp-eaters is affected by the mouth laterality of each individual, although the laterality of the prey (shrimp) that were hunted could not be determined. According to a theoretical study by Nakajima et al. (2004), situations in which predators can exploit more prey of the opposite laterality than ones of the same laterality drive alternation of the fitness advantage between two phenotypes, leading to frequency-dependent selection that maintains the dimorphism.

Furthermore, evidence for a genetic basis for abdominal dimorphism means that the frequencies of laterality types in a population at one time can affect that of the following generation. In several shrimp-eating cichlids (e.g., *Altolamprologus compressiceps* and *Gnathochromis pfefferi*) in Lake Tanganyika, the frequencies of the lateralities appear to have changed year by year during the last 10 years (Takeuchi and Hori, unpublished data). The mouth laterality of scale-eating cichlids is affected by both the frequencies of the laterality in the population and the frequencies of lateralities in prey species (Hori, 1993; Takahashi and Hori 1994). These findings imply that the frequencies of shrimp laterality types changes with the frequency of mouth lateralities in shrimp-eating cichlids. The laterality of shrimp may play an important role in the dynamics of these populations. Further investigations are required to examine the relationship between the laterality along generations in shrimp and that in shrimp-eating fish.

## ACKNOWLEDGMENTS

We thank the staff of the Lake Tanganyika Research Unit (LTRU), Department of Research and Specialist Services, Republic of Zambia, for providing facilities for field research, and especially J. Kitamura for his assistance in sampling of *L. latipes*. We specially thank M. Nishino for help with the taxonomy of the shrimps. We are grateful to M. Yasugi, R. Takahashi, T. Sota, K. Watanabe, Y. Takami, N. Nagata, and other members of the Laboratory of Animal Ecology, Graduate School of Science, Kyoto University for their valuable and critical comments on an early draft. Lastly we thank the editor and anonymous referees for their suggestions. Materials

in the Mizorogaike pond were collected under the permission of the Agency for Cultural Affairs to Dr. Yasuhiro Takemon for the restoration project of the Mizorogaike pond supported by Environmental Technology Development Fund from Ministry of the Environment. This study was partly supported by JSPS Research Fellowships for Young Scientists, the Grant for the Biodiversity Research of the 21st Century COE (A14), grants-in-aid for Scientific Research in Priority Areas (14087203), and the Global Center of Excellence Program "Formation of a Strategic Base for Biodiversity and Evolutionary Research: from Genome to Ecosystem," Ministry of Education, Culture, Sports, Science and Technology (MEXT), Japan.

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(Received October 21, 2007 / Accepted January 4, 2008)