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Inheritance Pattern of Lateral Dimorphism in Two Cichlids (a Scale Eater, *Perissodus microlepis*, and an Herbivore, *Neolamprologus moorii*) in Lake Tanganyika

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Antisymmetry in the direction of the mouth opening, to either the right (“lefty”) or left (“righty”), was documented in the scale-eating cichlid *Perissodus microlepis*. This study revealed the presence of lefty and righty mouth morphs in the herbivorous cichlid *Neolamprologus moorii*, although the degree of deviation was not large. Both species are biparental brooders and guard their young. We examined the inheritance pattern of the dimorphism (laterality) using parents and broods of *P. microlepis* and *N. moorii* collected in the wild. In *P. microlepis*, lefty-lefty pairs had a 2:1 frequency of lefty:righty young, lefty-righty pairs a similar number of each type of young, and righty-righty pairs only righty young. Similar inheritance patterns were observed in *N. moorii*. We propose two hypotheses to explain the inheritance pattern: Mendelian genetics with the lefty allele dominant over the righty and the dominant allele homozygous lethal, and cross-incompatibility that is pre-dominant in lefty homozygotes.

Key words: freshwater fish, behavior, inheriting pattern, morphotype

INTRODUCTION

Two morphological types in the direction of the mouth opening have been detected in scale-eating cichlid fishes from Lake Tanganyika (Liem and Stewarts, 1976; Hori, 1991, 1993). One type has its mouth opening to the right, due to a left lower jaw longer than the right (termed “lefty”), whereas the other type has its mouth to the left due to a longer right jaw (“righty”). Note that Hori has changed the definitions of lefty and righty to those described above (M. Hori, unpublished manuscript); in previous papers (Hori, 1991, 1993; Mboko *et al.*, 1998; Seki *et al.*, 2000), he considered an individual with its mouth-opening to the right to be “right-handed” or “dextral”. This dimorphism should be called “laterality”, in which there are no individuals with only a little deviation from symmetry, and differs from fluctuating asymmetry (see the definition in van Valen, 1962). Lateral dimorphism in mouth opening direction has been found in an herbivorous cichlid (Mboko *et al.*, 1998) and even in a freshwater omnivorous goby (Seki *et al.*, 2000), although the degree of deviation in these fish is not so large as in the scale eaters. These lateral dimorphisms are a typical example of antisymmetry (Palmer, 1996).

Hori (1993) showed that the lateral dimorphism in mouth

morph in the scale eater *P. microlepis* is heritable, determined by a simple Mendelian one-locus, two-allele system in which the lefty is dominant over the righty. The frequencies of F1 phenotypes, however, did not perfectly fit to expected values. As Hori (1993) pointed out, the brood samples he used possibly included young of other parents, because of the frequent occurrence of intraspecific brood-mixing through “farming-out” during the guarding period (Yanagisawa, 1985). For examination of the inheritance pattern of lateral dimorphism, a breeding pair and their genetic young should be used. However, in *P. microlepis* captured from the wild, it is difficult to identify the laterality of small F1 offspring before brood mixing occurs.

Seki *et al.* (2000) found that the freshwater goby *Rhinogobius flumineus* exhibits lateral dimorphism in mouth morph and examined the inheritance of this laterality using parental pairs and their young maintained in an aquarium. These authors suggested that the mouth dimorphism in this goby may be Mendelian, with the lefty morph dominant over the righty and the dominant allele homozygous lethal (Seki *et al.*, 2000). Differences reported in the inheritance systems between *P. microlepis* and *R. flumineus* could be either phylogenetic, or due to improper methodology used in the former case. In the present study, to accurately examine the inheritance system in *P. microlepis*, we collected parents and their broods in the early stage of guarding, and maintained the small young in an aquarium until they grew large enough for the identification of laterality.

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Our preliminary examination on the direction of the mouth opening in *Neolamprologus moorii*, an herbivorous cichlid in Lake Tanganyika, suggested that this fish likely also exhibits lateral mouth dimorphism. This fish is a biparental guarder, and neither sneaker males nor brood mixing through farming out have been reported (Karino, 1997, 1998). Thus, this fish should also be a good subject for examination of the inheritance system. Here we report on lateral dimorphism in the direction of the mouth opening in *N. moorii* and on the inheritance of the laterality in *P. microlepis* and *N. moorii*. Additionally, we discuss the relationship between morphological and behavioral laterality, based on an accumulating literature on behavioral laterality in fishes (e.g., Cantalupo *et al.*, 1995, 1996; Bisaza *et al.*, 1997; Miklosi *et al.*, 1998; Mboko *et al.*, 1998; Facchin *et al.*, 1999; Heuts, 1999; Bisazza *et al.*, 2000; Seki *et al.*, 2000; Tsujimoto, 2002).

MATERIALS AND METHODS

Neolamprologus moorii is a small cichlid (up to 9 cm TL) distributed in the southern part of Lake Tanganyika (Kohda and Takemon, 1996; Kohda *et al.*, 1996), while *P. microlepis* is ubiquitous around the lake. Fish samples of both species were obtained from the shallow rocky shore around Mpulungu, Zambia, using SCUBA. In both species, parents guard their brood in a compact assemblage <50 cm in diameter, on or above the nest site, which is variable in distance from the nests of conspecifics. The parents of a brood are easily identified through observation of their guarding behavior against brood predators (Yanagisawa, 1985; Karino, 1997, 1998).

In *P. microlepis*, females alone mouth-brood eggs and embryos for about 9 days, after which both parents jointly guard free-swimming young. To avoid broods including young of other parents, we selected broods of fry just after mouth brooding that were <12 mm in total length (TL) and were >5 m from the nearest conspecific brood. A total of 15 broods and their parents were col-

lected from 2002 to 2004 and were transported to the laboratory of the Lake Tanganyika Research Unit, Mpulungu, Zambia (LTRU). Parents were killed in chilled water and preserved in 10% formalin. The direction of the mouth opening of the fixed adults was readily apparent, as a figure and a photograph in Hori (1991, 1993) had indicated.

The young of a brood were maintained in the laboratory in a 40-L aquarium with aeration and were fed on Tetramine artificial flake food for 2 weeks to 2 months. The young were sampled in chilled water and measured, and their TL ranged from 13–22 mm. The joints of the lower jaw develop when the young are about 8 mm in TL, and the degree of deviation in the mouth asymmetry increases as the fish grow larger (Hori, personal observation). The direction of the mouth opening was checked under a binocular at 10X magnifi-

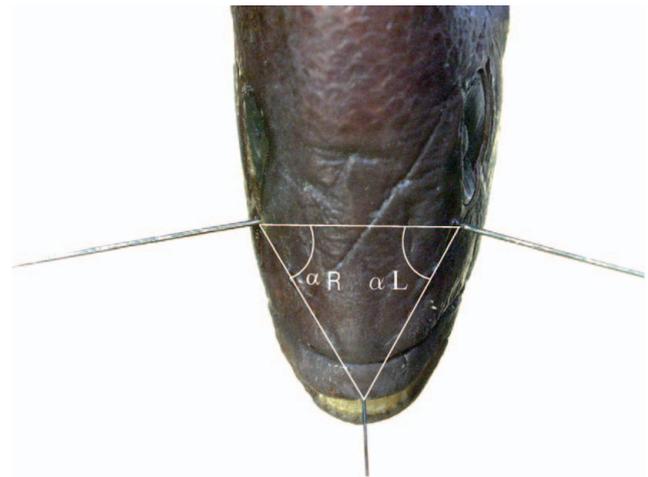


Fig. 1. Digital-microscope image of the head of *Neolamprologus moorii*, showing angles Alpha L and Alpha R.

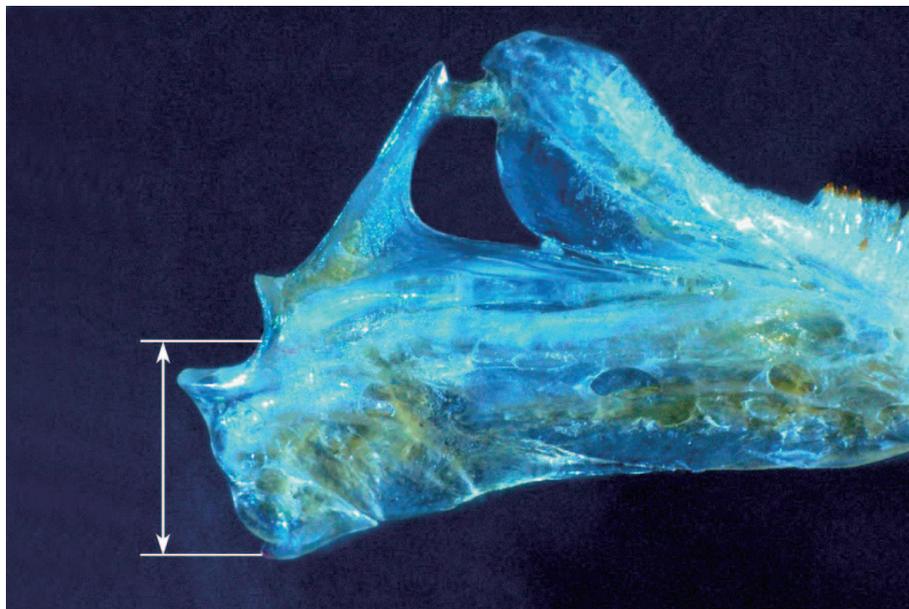


Fig. 2. Photograph of the posterior end of the mandible (right side) of *Neolamprologus moorii* showing the height measurement that was made. See text for a definition of this height.

cation, and was not difficult to discriminate in young fish >12 mm in TL.

The mouth opening of *N. moorii* deviated to a greater or lesser extent to either the left or the right. We visually examined individuals of *N. moorii* to determine which side of the head faced the front, and the side on which the mouth opened. The degree of deviation in the direction the mouth opened was not as large as in *P. microlepis*. Accordingly, we employed two quantitative methods to examine mouth laterality in *N. moorii*. The first was based on differences in the angle from the eye pits to the intersection of the two upper jaws. To measure the relevant angles, we used a digital microscope (VHX-100, Keyence Ltd.). On each image of a fish head, we drew a triangle connecting the frontal points of the two eye pits and the upper-jaw intersection, as shown in Fig. 1, and measured angles Alpha L and Alpha R to the nearest 0.1°. The value of Alpha L minus Alpha R was used as indicator of the laterality of each fish: a difference of 0 indicated symmetry and a large absolute value indicated a high degree of laterality in either direction. For this examination, we used 100 adult individuals collected around Mpulungu from 1988 to 1997 (45 females, mean±SD standard length (SL)=76.1±6.1 mm, range=58.3–93.1 mm; 55 males, 80.4±6.3 mm, 69.1–97.9 mm).

In the second quantitative method, we measured the height of each mandible at the posterior end, as the distance between the socket bottom of the suspensorial articulation facet of the anguloarticular and the ventral corner of the retroarticular (Fig. 2). Mandible ends were measured on 109 adult fish collected around Mpulungu in 2005 (63 males, 62.8–79.4 mm SL; 56 females, 64.5–79.3 mm). Before the examination, which side of the head faced the front and the side on which the mouth opened widely were recorded. Fish were killed in chilled water and their heads were boiled to obtain the mandibles. The heights of the left (Height L) and right (Height R) mandible ends were measured under the digital microscope (VHX-100, Keyence Ltd.). An index of asymmetry was calculated with the formula $(\text{Height R} - \text{Height L}) / (\text{Height R} + \text{Height L}) \times 2 \times 100$ (Palmer and Strobeck, 1986). For 18 of the 100 fish for which angles were measured, the heights were also measured to preliminarily examine the relationship between the two variables.

Both parents of *N. moorii* guard their brood until the young grow to 3 cm in TL (Karino 1997, 1998). To examine the inheritance of the mouth dimorphism, sets including both parents and their

brood were collected in 1996 and 1997. We collected a total of 27 brooding pairs and their broods. Young were captured with fine-mesh hand nets. Young were ≥ 20 mm in TL, and brood size ranged from 7–93. All broods were >2 m distant from neighboring conspecific broods. The adult fish were killed with an overdose of clove oil and were preserved in 10% formalin. Young were killed in chilled water and preserved in 10% formalin. The direction of the mouth opening of adults was determined by eye. The direction of the mouth opening in the young was determined under a binocular microscope at 10X magnification, as for *P. microlepis*.

RESULTS

Dimorphism in the mouth opening in *N. moorii*

Laterality in the angles of adult *N. moorii* is shown in Fig. 3. Individuals exhibited dimorphism regardless of sex, and the degree of deviation varied. No fish were distributed at the point of symmetry. The righty and lefty morphs judged by eye always corresponded to the laterality indicated by the angles: in the lefty, when the left side of the head faced more or less in front and the right side of the mouth opened widely, Alpha R was always larger than Alpha L, and vice versa in the righty.

Similar results were obtained from the mandible heights (Fig. 4). Individual *N. moorii* exhibited dimorphism, and the degree of the deviation varied, but no fish were distributed at the point of symmetry. The dimorphism corresponded with the righty and the lefty individuals in which the mouth-opening direction was determined by eye: Height R was smaller than Height L in the lefty and larger than Height L in the righty, except for one lefty female with a large Height R. There was a significantly strong correlation between the degree of difference in the angles and the index of asymmetry in mandible height ($Y=0.774+0.553X$, $R^2=0.568$, $p=0.0003$, $n=18$; Fig. 5).

Inheritance patterns in *P. microlepis* and *N. moorii*

In *P. microlepis*, when both parents were lefty, the

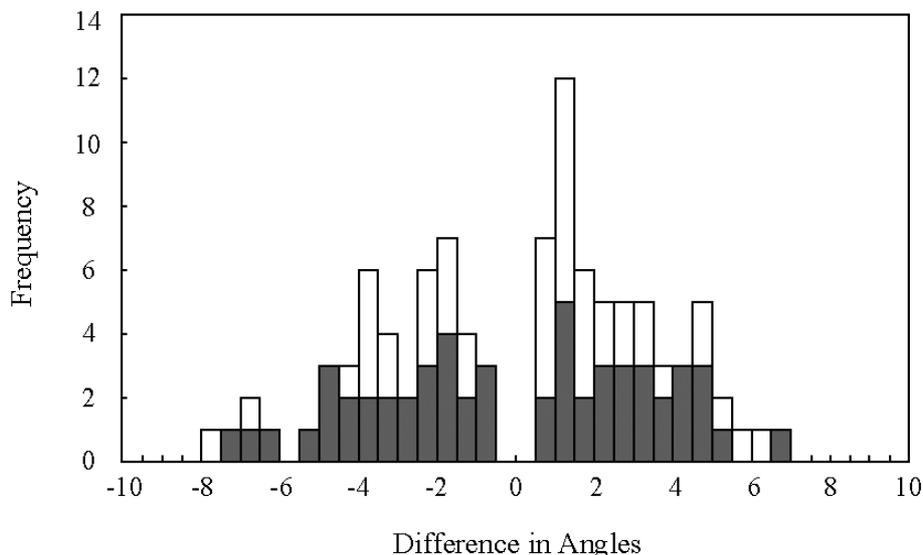


Fig. 3. Frequency distribution of individual differences in angles (Alpha L–Alpha R) in *Neolamprologus moorii*. Fish with negative values are lefty, with mouths opening toward the right. Open bars, females; filled bars, males.

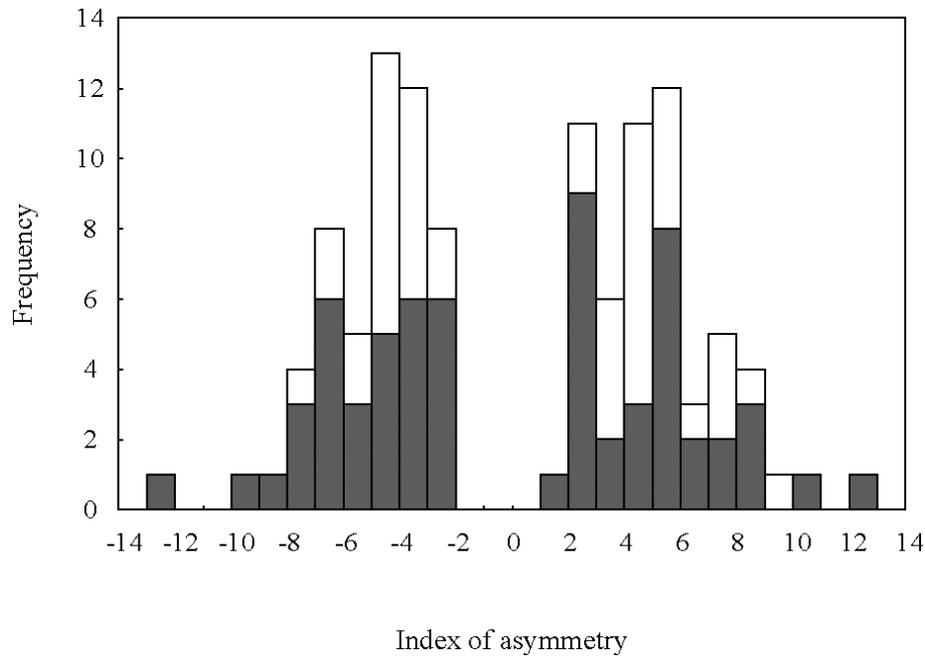


Fig. 4. Frequency distribution of the index $[(\text{Height R}-\text{Height L})/(\text{Height R}+\text{Height L})\times 2\times 100]$ of mouth laterality in *Neolamprologus moorii*. Fish with negative index values are lefty. Open bars, females; filled bars, males.

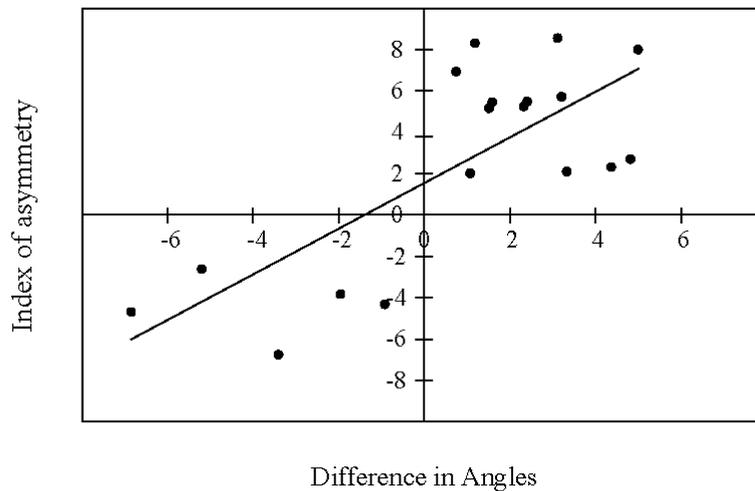


Fig. 5. Relationship between the difference in angles ($\text{Alpha L}-\text{Alpha R}$) and index of asymmetry in mandible height $[(\text{Height R}-\text{Height L})/(\text{Height R}+\text{Height L})\times 2\times 100]$ in *Neolamprologus moorii*. Male $n=10$; female $n=8$.

young exhibited a lefty:righty ratio of 2:1 (Table 1). In pairs of righty and lefty parents, the ratio of lefty:righty young was close to 1:1. The young of righty parents were of righty phenotype. If a simple Mendelian one-locus, two-allele system with lefty dominant over righty operates in *N. moorii*, the F1 phenotypic ratio from a LxL cross should be lefty:righty=3:1. The F1 phenotypic ratio from lefty parents was significantly different from 3:1 ($=821:274$; $\chi^2=26.4$, $p<0.0001$); the relative frequency of the lefty young was low. However, phenotypic frequencies were not significantly different from those expected under the hypothesis of a Mendelian one-locus, two-allele system with the dominant gene

homozygous lethal (Table 1).

The observed frequencies of the two morphs of young from three combinations of parents of *N. moorii* resembled those of *P. microlepis* (Table 1). The ratio of F1 phenotypes from righty parents was close to 2:1. The F1 phenotypic ratio was close 1:1 from righty and lefty parents, and all young from righty parents were righty. The F1 phenotypic ratio from lefty parents was likely different from lefty:righty=3:1 ($=84:28$; $\chi^2=35.2$, $p=0.06$). Phenotypic frequencies were consistent with those expected from the hypothesis (Table 1).

Table 1. Phenotype frequencies in broods of *Perissodus microlepis* and *Neolamprologus moorii* collected from wild. Expected ratios (Exp.) are hypothetically expressed from the phenotype combination of the pair, if the genetic pattern follows the Mendelian one-locus-two-alleles system with lefty (L) being dominant over righty (R) and the dominant gene acting as lethal when in a homozygote. The lefty parents are also assumed to be heterozygotes. Figures in parentheses in upper line are the number of pairs.

<i>P. microlepis</i>			
Parents	L×L (6)	L×R (6)	R×R (3)
F1	L:R	L:R	L:R
	71: 40	65: 59	0:263
	228:118	44: 36	0: 76
	95: 37	65: 71	0:140
	149: 66	186:201	
	99: 46	80: 86	
	67: 38	66: 83	
Total	709:385 (2:1.09)	506:536 (1:1.06)	0:479 (0:1)
Exp.	2:1	1:1	0:1

The phenotype frequency of F1 is not significantly different from expected value in the all parent combinations of L×L and L×R (χ^2 -test, in all combinations, $p>0.3$).

Continued

<i>Neolamprologus moorii</i>			
Parents	L×L (4)	L×R (15)	R×R (8)
F1	L:R	L:R	L:R
	21:14	44: 47	0:36
	6: 3	21: 18	0:19
	23:13	22: 26	0:35
	20:12	16: 20	0:53
		11: 13	0:11
		20: 22	0:35
		19: 18	0:10
		13: 17	0:35
		1: 6	
		8: 9	
		9: 10	
		19: 18	
		19: 22	
		12: 11	
		18: 18	
Total	70:42 (2:1.20)	252:275 (1:1.09)	0:234 (0:1)
Exp.	2: 1	1: 1	0:1

The phenotype frequencies of F1 are not significantly different from expected values in the all parent combinations of L×L and L×R except the two of young less than 10 in number (χ^2 -test, in all combinations, $p>0.6$).

DISCUSSION

Genetic basis of lateral dimorphism in mouth direction

The herbivorous *N. moorii* showed lateral dimorphism in mouth-opening direction, as do some other fish previously examined (Hori, 1991; Mboko et al., 1998; Seki et al., 2000). This laterality corresponded not only with the difference in the angles, but also with the index of asymmetry based on mandible posterior ends. This correspondence and the highly significant correlation between these two parameters

strongly support the existence of mouth laterality in *N. moorii*.

Our examination of the relationship in phenotypes between parents and young in *P. microlepis* and *N. moorii* revealed similar patterns: lefty parents produced young in a ratio of lefty:righty=2:1; lefty×righty parents produced young in a ratio of 1:1; and righty parents produced only righty young. The F1 phenotypic ratio from lefty parents in both species was inconsistent with that expected from a simple Mendelian system with lefty dominant over righty. A similar inheritance pattern of laterality has been reported in the freshwater goby *Rhinogobius flumineus* (Seki et al., 2000), where the F1 phenotypic ratio from lefty parents was also different from the ratio of lefty:righty=3:1 (235:143 vs. 284:94; $\chi^2=14.8$, $p<0.001$). In these three cases, the frequency of the lefty phenotype among F1s was lower than expected. Our results, however, might be accounted for by the hypothesis that mouth dimorphism in *P. microlepis* and *N. moorii* depends on a Mendelian system in which lefty is dominant over righty, with the dominant gene homozygous lethal; in this case, all lefty phenotypes should be heterozygous, as was suggested for the goby *R. flumineus* by Seki et al. (2000).

An alternative hypothesis is cross-incompatibility: lefty-lefty combinations will lead to fewer, less viable progeny from lefty-lefty crosses, while other mating combinations will produce normal progeny (Hurst et al., 1996; Jennions, 1997; Jeanne et al., 2003). The F1 phenotypic ratios we observed do not seem to fit this pattern in terms of quantitative genetics (Falconer, 1989).

We have no other hypotheses to account for the observed F1 phenotypic ratios in *P. microlepis*, *N. moorii*, and the goby (Seki et al., 2000). Mouth laterality is likely to be a rather common phenomenon in fish (Nakajima et al., 2004, 2005). The similarity of inheritance pattern in these three ecologically different and phylogenetically divergent species seems to suggest that the mode of inheritance will apply to other fish as well. The hypothesis of a lethal dominant allele allows the prediction that eggs from a pair of lefty parents will have a mortality 25% higher than those from the other two parental combinations, while this will not always be the case for the cross-incompatibility hypothesis.

In either hypothesis, if females can recognize the mouth laterality of potential mates, lefty females should prefer righty mates when other conditions of the males are the same, whereby mating will result in higher hatching success than otherwise. In contrast, righty females will not exhibit a preference in male laterality. This will be the same in the case of male mate choice. However, mate choice in the context of laterality would not be determined only by the mortality of the offspring, even if mate conditions were equal.

Oscillation in five-year cycles in the frequency of the dimorphism has been reported in a population of *P. microlepis* (Hori, 1993), and frequency-dependent selection was found empirically and theoretically to be the main force maintaining this oscillation (Hori, 1993; Takahashi and Hori, 1994, 1998). When the amplitude of the oscillation is large, individuals of the less numerous morph will have a significant advantage. In this case, young of the minor morph will be more valuable than young of major morph, and this minority advantage might affect mate choice. This prediction

about mate choice can be tested by laboratory experiments.

Lateral and behavioral dimorphism in fish

Mouth laterality in *N. moorii* clearly showed two peaks for each of the two indexes, on either side of the 0 point of symmetry, and no fish were plotted on the point of symmetry. This indicates that the laterality of this fish and some other species previously examined (Hori, 1991; Mboko *et al.*, 1998; Seki *et al.*, 2000) differs from fluctuating asymmetry (van Valen, 1962; Palmer and Strobeck, 1986; Leary and Allendorf, 1989). Either the righty or the lefty in *N. moorii* varied in deviation, similarly to the laterality in previous studies. The mouth laterality observed in *N. moorii* likely occurs in many other fishes (Nakajima *et al.*, 2004, 2005); 19 additional fish species examined seem to show this lateral dimorphism (M. Hori, unpublished data).

In the lefty of *N. moorii*, as in *P. microlepis* (Hori, 1993), the left side of the head faced more or less toward the front and the right side of the mouth opened widely, and vice versa in the righty. The mouth dimorphism in the scale-eaters (Hori, 1991, 1993) is clearly related to laterality in foraging behavior. In the herbivorous cichlid *T. temporalis*, the lefty tends to use the right side of the jaw more frequently, and the righty the left side (Mboko *et al.*, 1998); mouth usage in foraging by this fish seems to be related to the laterality. The goby *R. flumineus* usually stays on the bottom and bends the body in either direction. The curvature of the body toward the right or left corresponds with the mouth-opening direction (Seki *et al.*, 2000). These examples suggest that the mouth laterality, which is related to laterality in other morphological characters, is likely also related to behavioral laterality.

Heuts (1999) reports that in zebrafish, behavioral laterality in fast turns during swimming is related to the laterality of white and red muscle masses on either side of body; this is another example of morphological and behavioral lateralization. *Rhinogobius flumineus* shows individually biased direction of detour escape from a stimulus: a righty tends to turn to the right and a lefty equally in either direction (Tsujiimoto, 2002). This study implied that there might be a relationship between the mouth-opening direction and laterality in muscle masses in *R. flumineus*, a possibility that can be tested by anatomical examination. Bissaza and his colleagues have studied laterality in fish behaviour (Cantalupo *et al.*, 1995, 1996; Bisazza *et al.*, 1997; Facchin *et al.*, 1999; Bisazza *et al.*, 2000). For example, *Jenynsia lineata* exhibits individually consistent laterality during escape behavior (Bissaza *et al.*, 1997). Behavioral laterality in fighting and courting in individual betta fish is consistent for considerable periods (Cantalupo *et al.*, 1996). Such individually consistent behavioral laterality could be related to anatomical lateral dimorphism, as observed in the goby *R. flumineus* (Seki *et al.*, 2000; Tsujiimoto, 2002) and in cichlids (Hori, 1993; Mboko *et al.*, 1998).

In conclusion, not only scale-eaters but also other fishes show genetically based laterality in the direction of the mouth opening. This antisymmetry is associated with other lateral dimorphisms, such as in muscle mass and some sensory abilities, which may cause periodic fluctuations of morph frequencies in populations through intra- and inter-specific behavioral interactions, as shown in scale eaters

(Hori, 1993) and predicted theoretically (Takahashi & Hori, 1994, 1998; Nakajima *et al.*, 2004, 2005). The genetic bases of laterality and the mechanism by which the dimorphism is maintained should be examined in many other fish taxa across a variety of habitats.

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REFERENCES

- Bissaza A, Cantalupo C, Vallortigara G (1997) Lateral asymmetries during escape behavior in a species of teleost fish (*Jenynsia lineata*). *Physiol Behav* 61: 31–35
- Bisazza A, Cantalupo C, Capocchiano M, Vallortigara G (2000) Population lateralization and social behaviour: a study with 16 species of fish. *Laterality* 5: 269–284
- Cantalupo C, Bisazza A, Vallortigara G (1995) Lateralization of predator-evasion response in a teleost fish (*Girardinus falcatus*). *Nueropsychologia* 33: 16737–16746
- Cantalupo C, Bisazza A, Vallortigara G (1996) Lateralization of displays during aggressive and courtship behaviour in the Siamese fighting fish (*Betta splendens*). *Physiol Behav* 60: 249–252
- Facchin L, Bissaza A, Vallortigara G (1999) What causes lateralization of detour behaviour in fish? Evidence for asymmetries in eye use. *Behav Brain Res* 103: 229–234
- Falconer DS (1989) *Introduction to Quantitative Genetics*. 3rd ed, Longman Group UK, London
- Heuts BA (1999) Lateralization of trunk muscle volume, and lateralization of swimming turns of fish responding to external stimuli. *Behav Proc* 47: 113–124
- Hori M (1991) Feeding relationships among cichlid fishes in Lake Tanganyika; effects of intra- and interspecific variations of feeding behavior on their coexistence. *INTECOL Bull* 19: 89–102
- Hori M (1993) Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science* 260: 216–219
- Hurst, LD, Atlan A, Bengtsson BO (1996) Genetic conflicts. *Q Rev Biol* 71: 317–364
- Jeanne A, Zeh D, Zeh W (2003) Toward a new sexual selection paradigm: polyandry, conflict and incompatibility. *Ethology* 109: 929–950
- Jennions MD (1997) Female promiscuity and genetic incompatibility. *Trends Ecol Evol* 12: 251–253
- Karino K (1997) Influence of brood size and offspring size on parental investment in abiparental cichlid fish, *Neolamprologus moorii*. *J Ethol* 15: 39–43
- Karino K (1998) Depth-related differences in territory size and defense efficiency in the herbivorous cichlid, *Neolamprologus moorii*, in Lake Tanganyika. *Ichthyol Res* 45: 89–94
- Kohda M, Takemon Y (1996) Group foraging by the herbivorous cichlid fish, *Petrochromis fasciatus*, in Lake Tanganyika. *Ichthyol Res* 43: 55–63
- Kohda M, Yanagisawa Y, Sato T, Nakaya K, Niimura Y, Matsumoto K, Ochi H (1996) Geographical colour variation in cichlid fishes at the southern end of Lake Tanganyika. *Env Biol Fish* 45: 237–

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- Leary RF, Allendorf FW (1989) Fluctuating asymmetry as an indicator of stress: implications for conservation biology. *Trends Ecol Evol* 4: 214–217
- Liem KF, Stewart DJ (1976) Evolution of the scale-eating cichlid fishes of Lake Tanganyika: a generic revision with a description of a new species. *Bull Mus Comp Zool* 147: 319–350
- Miklosi A, Andrew RJ, Savage H (1998) Behavioural lateralization of the tetrapod type in the zebrafish (*Brachydanio rerio*). *Physiol Behav* 63: 127–135
- Mboko SK, Kohda M, Hori M (1998) Asymmetry of mouth-opening of a small herbivorous cichlid fish *Telmatochromis temporalis* in Lake Tanganyika. *Zool Sci* 15: 405–408
- Nakajima M, Matsuda H, Hori M (2004) Persistence and fluctuation of lateral dimorphism in fishes. *Am Nat* 163: 692–698
- Nakajima H, Matsuda H, Hori M (2005) A population genetic model for lateral dimorphism frequencies in fishes. *Popul Ecol* 47: 83–90
- Palmer AR, Strobeck C (1986) Fluctuating asymmetry: measurement, analysis, pattern. *Rev Ecol Syst* 17: 391–421
- Palmer, AR (1996) From symmetry to asymmetry: phylogenetic patterns of asymmetry variation in animals and their evolutionary significance. *Proc Natl Acad Sci USA* 93: 14279–14286
- Seki S, Kohda M, Hori M (2000) Asymmetry of mouth morph of a freshwater goby, *Rhinogobius flumineus*. *Zool Sci* 17: 1321–1325
- Takahashi S, Hori M (1994) Unstable evolutionarily stable strategy and oscillation: a model of lateral asymmetry in scale-eating cichlids. *Am Nat* 144: 1001–1020
- Takahashi S, Hori M (1998) Oscillation maintains polymorphism - a model of lateral asymmetry in two competing scale-eating cichlids. *J Theor Biol* 195: 1–12.
- Tsujimoto H (2001) Asymmetry of the river lizard goby, *Rhinogobius flumineus*. MS Thesis, Osaka City University
- Yanagisawa Y (1985) Parental strategy of the cichlid fish *Perissodus microlepis*, with particular reference to intraspecific brood 'farming out'. *Environ Biol Fish* 12: 241–249
- Van Valen L (1962) A study of fluctuating asymmetry. *Evolution* 16: 125–142

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