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Scale-Eating in *Perissodus microlepis* (Cichlidae) and Change of Its Food Habits with Growth

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Abstract Scale-eating behaviour of *Perissodus microlepis* was observed in its natural habitat and the stomach contents of individuals at various developmental stages were examined. Young guarded by the parents fed on zooplankters, and juveniles exploited a wide variety of food items: zooplankters, phytoplankters, benthic animals and scales of other fishes. Adults subsisted primarily on scales. Adult *P. microlepis* removed scales from diverse fish species, most intensively from algae-eating cichlids larger than themselves and with flat bodies. Most of their attacks were delivered from near the substrate. They sometimes ambushed their prey using the underside or crevice of a rock as cover. Fishes engaging in feeding, territorial attacking or courtship display were often attacked.

The cichlids of the African lakes exhibit a great diversity of feeding habits (Fryer, 1959; Greenwood, 1964; Fryer and Iles, 1972). Scales of living fishes are exploited by some cichlids endemic to Lake Victoria, Lake Tanganyika or Lake Malawi, indicating that the scale-eating habit has independently evolved several times (Fryer and Iles, 1972). *Perissodus microlepis* is one of the seven species known as scale-eaters in Lake Tanganyika (Poll, 1956; Liem and Stewart, 1976). Brichard (1978) and Kawanabe (pers. comm.) observed scale-eating behaviour of this fish in the field. The latter observed that it succeeded in ripping off scales from prey fishes when they were busy in territorial attacking or sexual display. However, no quantitative observation has been carried out on the behaviour of *P. microlepis* and their prey.

In the present study, we observed quantitatively the scale-eating behaviour of adult *P. microlepis* and situations and reactions of prey fishes when they were attacked. Prey-species preference by *P. microlepis* was also analyzed, comparing the numbers of observed attacks on respective species with their relative densities in the field. Stomach contents of this fish at various developmental stages were examined to analyze the degree of specialization of its food habits.

Materials and methods

The field work was carried out at rocky shore of Uvira, Luhanga and Mpemba situated at the northern end of Lake Tanganyika during the period from August to November 1981, in February 1982 and from August to November 1983. SCUBA was used in all observations and collections. Adult *P. microlepis* floated in midwater or wandered near the substrate shallower than 20 m. Floating adults were usually less active in scale-eating. Fifty nine adults wandering near the substrate were followed and observed for 60 min, keeping 2–5 m from them. When they succeeded in removing scales from prey fishes, the sites from which they started a dash and the situations of the prey fishes just prior to being attacked (e.g., solitary or schooling, or moving or stationary) were recorded. The sites were categorized into midwater and substrate, and the latter was still divided into six categories: the top, lateral side, underside and crevice of a rock, the ravine between rocks, and the other substrates (stones, gravel, sand and so on). We sometimes could not identify species of *Petrochromis*, *Ophthalmotilapia* and *Simochromis* for certain in the field, so those of each genus were lumped. To estimate the prey-species preference by *P. microlepis*, the numbers of cichlids in a 20×20 m^2 quadrat (0–12 m depths) at Luhanga counted by the Japanese team in January and February 1980 (Hori *et al.*, 1983) and December 1983 (unpublished data) were used as the relative densities of prey fishes in the study areas.

Specimens of *P. microlepis* were collected with

Table 1. Sites from which *Perissodus microlepis* started a dash to attack prey fishes.

Sites	Rock					Other substrates	Midwater	Total
	Top	Lateral side	Underside	Crevice	Ravine			
Number of attacks	92	34	13	28	43	164	124	498
Frequency (%)	18.4	6.8	2.6	5.6	8.6	32.9	24.9	100

hand-nets and a gill-net. Stomach contents of 207 non-brooding adults and juveniles and 93 young guarded by the parents were examined. To analyze them, the occurrence method and, in part, the number method were used.

Caloric value of scales was measured with an oxygen bomb calorimeter by using scales from two *Petrochromis polyodon* (89 and 93 mm SL), two *Tropheus moorei* (73 and 79 mm) and three *Cyathopharynx furcifer* (81, 86 and 106 mm).

Results

Scale-eating behaviour. Adult *P. microlepis* wandered above rocks, moving 20 to 70 m in an hour. They succeeded in striking at prey fishes 853 times during the 3,200 min observation period. *P. microlepis* stealthily approached its prey or ambushed. Just prior to making an attack, it usually stopped for a moment at a particular site and directed its head towards the prey. Dark stripes on its body faded before attacking, resulting in the reduction of conspicuousness. It dashed horizontally or slightly upwards and struck at the flank of the prey from a perpendicular or posterior position. The dislodged scales, if scattered in the water, were immediately picked up as they sank. The length of a dash was between 20 and 200 cm.

Sites from which it started a dash are shown in Table 1. Seventy five percent of attacks were from the substrate, though it stayed on the substrate only 66 percent of the observation period. It frequently started a dash from the top or lateral surface of a rock after approaching the prey along the rock surface. The undersides and crevices of rocks or the ravines between rocks were sometimes used as cover for ambush.

Twenty three species and species-groups suffered attacks by *P. microlepis* (Table 2). Only four are non-cichlid: *Lamprichthys tanganicanus* (Cyprinodontidae), *Lates microlepis* (Centropomidae) and *Varicorhinus tanganicae* and *Barilius moorei* (Cyprinidae). Attacks on cichlids amounted 89 percent of the total. The epilithic algae-eaters *Tropheus moorei* and *Petrochromis* spp. were most frequently attacked, followed by *Ophthalmotilapia* spp. and *L. tanganicanus* hovering near rocks.

To estimate a prey-species preference by *P. microlepis*, the numbers of adult cichlids in the quadrat at Luhanga were compared with the numbers of attacks observed (Table 2). The numbers of non-cichlids in the quadrat were not available. Frequencies of observed attacks on cichlid species of smaller body sizes than adult *P. microlepis* were much lower than expected when it is presumed that the frequency of attacks on each species are in proportion to its relative density (Table 3). A small species *Lamprologus brichardi*, which swarmed near rocks, though amounting to 71 percent of all cichlids in number, was only rarely attacked (7 percent of the total). Small benthic fishes, *Telmatochromis bifrenatus* and *T. temporalis*, were also very common but were very rarely attacked (Table 2). Among cichlids whose adults were larger than, or as large as, adult *P. microlepis*, those with great body depths were selectively attacked (Table 3). Omnivorous cichlids, including pelagic species *Ophthalmotilapia* spp., seem to have been selectively attacked (Table 3), but this elucidation is probably not true because the densities of pelagic fishes are apt to be underestimated owing to their cautiousness. When herbivorous and carnivorous cichlids are compared, the former were more frequently attacked relative to their densities ($\chi^2=10.8$, $P<0.01$). Of 15 species which suffered no attack, 14 were carnivorous. Attacks on *Lobochilotes labiatus*, *Gnathochromis pfefferi* and *Lamprologus callipterus*, which were cruising individually or more often in a group in a wide area (Hori, 1983), were frequent relative to their densities, though they are carnivorous. Carnivorous cichlids *Lampro-*

Table 2. Frequencies of attacks by *Perissodus microlepis* on prey fishes and their adult sizes (A, >130 mm SL; B, 80–130 mm; C, <80 mm), body depth rates (L, >30% of SL; S, <30%), food habits (H, herbivorous; O, omnivorous; C, carnivorous) and relative densities in the field.

Species	Adult size	Body depth rate	Food habits	Relative density (%) (N=3,202)	Frequency of attacks (%) (N=853)
Tropheus moorei	B	L	H	3.44	22.7
Petrochromis spp.	A	L	H	1.91	21.0
Ophtalmotilapia spp.	B	L	O	0.87	12.2
Lamprichthys tanganicanus	B	L	C	—	8.4
Simochromis spp.	B	L	H	0.56	6.9
Lamprologus brichardi	C	L	C	71.34	6.2
Lobochilotes labiatus	A	L	C	0.02	4.9
Lamprologus elongatus	A	S	C	0.23	3.4
Gnathochromis pfefferi	B	L	C	0.09	2.7
Lamprologus modestus	B	L	C	0.45	2.0
Lamprologus callipterus	B	S	C	0.04	1.5
Eretmodus cyanosticus	C	L	H	1.46	1.4
Varicorhinus tanganicae	A	S	H	—	1.3
Telmatochromis temporalis	C	L	O	4.43	1.1
Lates microlepis	A	L	C	—	0.8
Lamprologus leleupi	B	S	C	0.40	0.7
Asprotilapia leptura	B	S	H	0.79	0.7
Limnotilapia dardennei	A	L	O	0.08	0.6
Barilius moorei	A	S	O	—	0.4
Lamprologus compressiceps	B	L	C	0.04	0.4
Lamprologus toae	C	L	C	0.19	0.4
Haplotaxodon microlepis	A	S	C	0.05	0.2
Lamprologus attenuatus	B	S	C	0	0.1
Telmatochromis bifrenatus	C	S	C	9.01	0
Lamprologus savoryi	C	L	C	1.23	0
Tanganicodus irsacae	C	L	C	1.17	0
Julidochromis marlieri	B	S	C	0.45	0
Perissodus microlepis	B	S	C	0.45	0
Lamprologus furcifer	B	S	C	0.38	0
Lamprologus tretocephalus	C	L	C	0.27	0
Lamprologus lemairei	A	L	C	0.16	0
Xenotilapia flavipinnis	C	S	C	0.14	0
Julidochromis transcriptus	C	S	C	0.13	0
Cyathopharynx furcifer	A	L	O	0.12	0
Telmatochromis caninus	A	L	C	0.05	0
Perissodus straelini	B	L	C	0.02	0
Lamprologus profundicola	A	L	C	0.02	0
Cyphotilapia frontosa	A	L	C	0.02	0

logus furcifer, *L. leleupi* and *Julidochromis marlieri*, which remained close to the rock surface and frequently retreated into a hole or crevice, were never or very rarely attacked. *P. microlepis* never attacked conspecifics (Table 2).

Situations of prey fishes when attacked by *P. microlepis* are shown in Table 4. One-fifth of the attacks were directed to schooling individuals. Solitary individuals passing in front of *P. microlepis* were most commonly attacked. The territorial algae-eaters *Tropheus moorei* and *Petrochromis* spp. were often attacked while they were feeding or chasing intruders. A male of *Lamprichthys tanganicanus* leading a female to its spawning site (a narrow crevice of rock) was a good attack objective for *P. microlepis*.

Table 3. Prey-species preference by *Perissodus microlepis* in relation to body sizes, body depth rates and food habits of prey fishes. Expected values are set in proportion to the relative densities in the field.

	Body size			
	>130 mm SL (10 spp.)	80–130 mm SL (14 spp.)	<80 mm SL (10 spp.)	Total
Observed	257	426	77	760
Expected	20.2	60.6	679.2	760

$\chi^2=5{,}513$, $P<0.001$.

	Body depth rate in species exceeding 80 mm SL		
	Large (>30% of SL) (15 spp.)	Small (<30%) (9 spp.)	Total
Observed	626	57	683
Expected	503.9	179.1	683

$\chi^2=113$, $P<0.001$.

	Food habits in species exceeding 80 mm SL			
	Herbivorous (4 spp.)	Omnivorous (3 spp.)	Carnivorous (17 spp.)	Total
Observed	438	109	136	683
Expected	430.1	68.7	184.2	683

$\chi^2=78$, $P<0.001$.

Table 4. Situations of prey fishes when attacked by *Perissodus microlepis*.

Species	Solitary					Schooling		Total
	Feeding	Territorial attacking	Courtship display	Passing	Motionless	Moving	Stationary	
Petrochromis spp.	40	14	3	74	17	18	19	185
Tropheus moorei	35	46	8	45	10	29	11	184
Ophthalmotilapia spp.	13	4	0	31	8	11	21	88
Lamprologus brichardi	17	0	0	26	0	0	15	58
Lamprichthys tanganicanus	1	5	26	20	2	0	0	54
Lobochilotes labiatus	10	1	0	19	6	5	0	41
Simochromis spp.	0	3	1	26	5	0	0	35
Lamprologus elongatus	1	1	0	7	5	2	4	20
Gnathochromis pfefferi	3	0	1	14	0	0	2	20
Lamprologus modestus	2	4	0	6	2	4	2	20
Others	12	3	0	34	11	6	2	68
Total	134	81	39	302	66	75	76	773

Prey fishes, however, never let the scale-eater do as it liked. They took precaution against its approach. When they witnessed it in the vicinity, they either drove it off or kept away from it. Territorial fishes such as *T. moorei* and *Petrochromis* spp. most severely chased it. Young fishes smaller than the scale-eater often showed a defensive display against it by expanding the unpaired fins. *P. microlepis* being detected by prey fishes usually moved to another place and watched for other chances of attacking.

Table 5. Stomach contents of *Perissodus microlepis*. f, frequency of occurrence in percent; n, mean number; m, maximum number.

		Young			Juvenile and Adult							
Size class (mm SL)		<10	<20	<30	<30	<40	<50	<60	<70	<80	<90	<100
No. examined		27	31	35	14	21	9	13	34	82	29	5
	f				28.5	61.0	100	84.6	85.3	100	100	100
Scales	n				18.5	5.0	46.5	69.6	158.2	146.1	152.0	182.2
	m				111	49	137	281	867	536	534	296
	f	96.3	93.5	94.3	78.6	95.2	33.3	15.4	17.6	17.1	10.3	20.0
Copepods	n	186.8	869.7	930.1	160.4	9.7	23.5	3.8	82.1	53.4	15.4	10.4
	m	810	2330	3088	1237	26	138	38	895	1189	333	52
	f	37.0	29.0	28.6	28.6	52.4	11.1					
Copepod nauplii	n	42.9	4.2	5.0	12.1	10.0	2.6					
	m	382	23	26	86	75	24					
	f		3.2	8.6	14.2	9.5			8.8	4.9	6.9	
Ostracods	n		2.0	0.8	0.4	0.2			1.9	0.4	2.3	
	m		64	6	5	4			57	21	67	
	f	14.8	51.6	62.9	78.6	66.7	11.1		17.6	7.3	3.4	
Atyid shrimps	n	0.8	2.8	4.0	3.6	4.8	1.1		8.5	1.1	1.0	
	m	10	18	13	9	35	10		121	26	30	
	f			5.7	7.1	4.8			20.6	7.3	3.4	
Chironomid larvae	n			0.1	0.2	0.1			3.3	0.6	0.4	
	m			3	4	3			51	16	12	
	f									2.4	3.4	20.0
Fish larvae	n									0.2	0.4	0.2
	m									7	13	1
Algae	f		22.5		35.7	100	33.3	46.1	14.7			
Undetermined filaments	f		6.4	2.8	35.7	46.7			14.7	13.4	17.2	20.0
Animal debris	f		16.1	5.7	7.1		33.3		50.0	26.8	48.2	40.0
Sand	f	77.7	12.9	8.5	7.1	42.8	22.2		14.7	7.3	31.0	20.0

The number of attacks which one individual of prey fish suffered was not observed in this study, but Mr. K. Yamaoka recorded it in some algae-eating cichlids in the Luhanga quadrat in 1980 and 1981 (unpublished data), while observing their feeding behaviour (Yamaoka, 1982, 1983). *Petrochromis fasciatus* was attacked once in 564 min observation but *P. polyodon* and *T. moorei* were never attacked in 975 and 260 min observations, respectively. This suggests that each individual of prey fish suffers little from the attack of *P. microlepis*.

Stomach contents. The young guarded by the parents (see Yanagisawa and Nshombo (1983) for their behaviour) mainly feed on copepods, copepod nauplii and other zooplankters (Table 5). Scales never occurred in their stomachs. The presence of sand in their stomachs indicates that they also pick up materials from the substrate. In underwater observations, we often saw the young make oral contact with the surface of their parents' bodies. This behaviour has already been reported in some other cichlids and it has been considered that the young obtain the mucus from the parents (Noakes and Barlow, 1973; Noakes, 1979). This behaviour of *P. microlepis* also may have a trophic function, though we could not detect mucus-like materials in the stomach contents.

The juveniles less than 60 mm SL, some of which are schooling and others solitary, take a wide variety of items. They feed on phytoplankters, zooplankters, benthic animals and scales (Table 5). Unidentified filamentous materials were also abundantly found in their stomachs. Most of the phytoplankters were the green algae *Anabaena flosaquare*, whose dense surface accumulations were observed in October 1981. At the northern end of the lake, a bloom of this algae occurs in September and October

Table 6. Relationship between standard length of *Perissodus microlepis* and diameter of scales in its stomach. Two-hundred scales were measured for each size-class.

Size of fish (mm SL)	50–60	<70	<80	<90	<100
No. specimens	3	2	10	4	3
Mean diameter (mm)	2.08	2.53	2.78	3.06	3.47
±S.E.	±0.13	±0.18	±0.14	±0.18	±0.21
Maximum diameter	4.5	5.5	5.75	6.5	8.5

every year (Dubois, 1958; Hecky *et al.*, 1981). Copepods, nauplii and ostracods eaten by juveniles were fewer than those eaten by the young guarded by the parents. About a half of the juveniles were taking scales, but the number of scales in one stomach was much smaller than that of scales eaten by an adult.

Scales were almost always found in the stomachs of adults more than 60 mm SL (Table 5). The maximum number in one stomach was 867. Scales in a stomach are tightly piled up like a pack of cards. They become thin and soft in the posterior part of the stomach and are converted into a white paste at the end of the intestine, indicating that they are digested. The mean diameter of scales in a stomach increases as the body size of the fish increases (Table 6). About 20 percent of adults examined were taking some zooplankters, but copepod nauplii were never found. Fish larvae, probably of *Lamprichthys tanganicanus*, were found in 4 adults.

Caloric value of scales. Caloric values of scales from *P. polyodon*, *T. moorei* and *C. furcifer* were 2,210, 1,779 and 2,250 cal g·dry wt^{-1}. The average was 2,080 cal g·dry wt^{-1}.

Discussion

Brichard (1978) mentioned that *P. microlepis* was seen "always in mid-water and not near the rock shore". Certainly, this fish spends much of its time in the water column. However, we observed that it came down to the substrate very often and three quarters of attacks on prey fishes were made from the substrate. To come in contact with the substrate is obviously one tactics for approaching prey without being noticed. For this purpose it exploits additional tactics; it ambushed using the shady sides of rocks as cover and selectively directed its attacks to fishes engaging in feeding or social activity. Fading its body stripes before attacking may also serve for this purpose. Since prey either counterattacks the predator or escapes from it if they can notice its approach beforehand, these tactics may be prerequisite for successful attacking.

P. microlepis removed scales from many fish species. But its preference for fishes larger than, or as large as, itself and for those with deep body shape are obvious (Table 3). The preference for the former is common to the majority of scale-eating fishes (Fryer and Iles, 1972; Major, 1973; Sazima, 1983) and the preference for the latter is indicated in *Therapon jarbua* (Whitfield and Blaber, 1978). A large target area such prey provide may be a primary reason for these preferences. Frequent attacks on algae-eaters, such as *Tropheus moorei*, *Petrochromis* spp. and *Simochromis* spp., may be in part due to their feeding activity on the open rock surface (see Yamaoka, 1982) other than the above features. This contrasts with very rare attacks on the carnivores *Lamprologus furcifer*, *L. leleupi* and *Julidochromis marlieri* which remain close to the more or less sheltered rock substrate.

Juvenile *P. microlepis* take a wide variety of food items besides scales but the adults mainly feed on scales. Such change in diet with growth is also known in the characoid scale-eater *Roeboides* (Roberts, 1970; Sazima, 1983). The majority of adult *P. microlepis*, however, take other food at the same time. In one case, more than a thousand copepods occurred in a stomach (Table 5). Parents guarding young were seemingly more dependent on zooplankters than were solitary adults, owing to the limitation of their movements, though not quantitatively ascertained yet. *P. microlepis* is a specialized scale-eater but is still euryphagous, as are most of the other lepidophagous fishes (Roberts, 1970; Zaret and Rand, 1971; Sazima, 1977, 1983).

The caloric value of scales measured in the

present study (=2 cal·mg^{-1}) is nearly equal to that from other fish (Whitfield and Blaber, 1978). Mucus covering the scales is said to be rich in protein and lipids (Wessler and Werner, 1957; Lewis, 1970). Here we tentatively compare feeding efficiency between scale-eating and feeding on zooplankters. An area of prey's scales dislodged by an attack of *P. microlepis* is estimated to be 50 mm^2, which was calculated from the area covered by teeth-marks when the mouth of adult was fully open. This value is equivalent to 6 mg, when measured in *Tropheus moorei* and *Cyathopharynx furcifer*. Therefore, the caloric value of scales obtained by one attack is about 12 cal. On the other hand, one zooplankter contains about 0.03 cal, provided its caloric value being 5.5 cal·mg^{-1} and the mean weight of one individual being 0.005 mg (an estimation from a common copepod *Mesocyclops leuckarti*). Accordingly, scales obtained by one attack correspond to some 400 zooplankters in calorie. For the planktivore *Lamprologus brichardi* inhabiting the same area as *P. microlepis*, it took 5.8 min on average to pick up 400 plankters during the daytime 0800 and 1600 (Gashagaza, unpublished data). This value is not much different from the time required for one successful attack by *P. microlepis* observed in this study (=3.75 min). This suggests that scale-eating has a comparable feeding efficiency to feeding on zooplankters.

Scales are easily renewable through regeneration (Sazima, 1983). So, scales may be one of the most stable food resources in the habitats where many fishes inhabit together. The parallel adoptions of scale-eating habit in a number of fish species in both freshwater and the sea (see Sazima, 1983) may be attributed to this feature.

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カワスズメ科魚類 *Perissodus microlepis* の「ウロコ食い」の習性と成長に伴う食性の変化

Muderhwa Nshombo・柳沢康信・名越　誠

タンガニイカ湖に生息する *Perissodus microlepis* の「ウロコ食い」の行動を自然状態で観察した．また，種々の発育段階の個体の胃内容物を調査した．親によって保護されている稚魚は主に動物プランクトンを摂餌し，親から独立後の未成魚は，他魚のウロコのほかに動物・植物プランクトン，底生動物を摂餌した．成魚は，多くの魚種（特に，大型で体高の高い付着藻類食魚）からはぎとったウロコを主要な餌としていた．ウロコをとるための攻撃は主に基底近くから行われ，時には，岩の下面やくぼみで待ち伏せた．近くを通過した魚のほかに，摂餌・ナワバリ行動・求愛行動にかまけている魚をよく襲った．

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