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Aggressive Behaviour and Dominance Relationships of the Dark Chub, *Zacco temmincki* with Special Reference to Their Individual Recognition

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Abstract Aggressive behaviour and dominance relationships of *Zacco temmincki* were observed by introducing fish into an enclosed pond. Chase (-flee), lateral display, parallel swim and butt were the principal behavioural patterns in aggressive encounters between fish, while chase, resulting in lateral display by the chased fish was the most common behavioural sequence. Initially, mutual behavioural patterns such as parallel swim and mutual lateral display were most evident among the total aggressive acts although chase became dominant three days after introduction into the pond. The dominance matrix constructed from chase-flee interactions during all observation periods contained many reverse attacks (336 out of 2,740 chases). These reverse attacks did not concentrate upon a specific period and were not site-dependent. Examination of chase-flee interactions and the subsequent behavioural pattern revealed that a chased fish reacted to the chaser either by attacking in turn, or performing lateral display etc. roughly in relation to the dominance rank of the chaser. This result implies that fish recognized each other to a great extent during aggressive encounters. It seems likely that such individual recognition was initiated during the early period when mutual behaviour was most frequent, and that some attacks against the dominance order were caused as a result of revolts rather than mistakes.

Individual recognition, which is defined in this study as some kind of discrimination of an individual from other members in a group, has been referred to as the stabilizing factor of a dominance hierarchy (Guhl, 1953; Morisita, 1976; Colgan, 1983). However, as Breed and Bekoff (1981) point out, it is difficult to demonstrate individual recognition in the context of a dominance hierarchy without designing experiments with isolated individuals. Some studies proved the ability of fish to recognize every other individual by experiments (Goz, 1941; Todd *et al.*, 1967; Todd, 1971; Fricke, 1973; Fricke and Holzberg, 1974). On the other hand, it is well known that the dominance order of fish has an unstable nature with reverse attacks or circular relationship, which implies the deficiency or scarcity of mutual recognition (Brown, 1975; Wilson, 1975; Morisita, 1976). In some fishes, individual recognition has been suggested to function in the dominance hierarchy (Braddock, 1945; Nelson, 1964; Erickson, 1967; Gorlick, 1976). These arguments are based on the facts that the dominance order is fairly straight rather than confused and certain fish preferentially chase or avoid certain other fish. Further quantitative analysis of inter-individual relationships is required in the context of a hierarchy in order to clarify the mechanism of dominance relationships including individual recognition.

In a previous paper (Katano, 1983), I showed that a dominance order of male *Z. temmincki* functions in the mating activities under natural conditions. Further observations of the aggressive encounters of the fish were conducted in the summer of 1981 by means of introducing fish into an outdoor enclosed pond. The purpose of this paper is to describe the details of the aggressive behaviour of the fish with special reference to individual recognition. This was not confirmed in the previous field study.

Materials, methods, and study area

On August 11, 1981, prior to the experiment, six transparent columnar baited traps were placed in different pools in the Takano River near Yase, Kyoto City. Ten individuals, which could easily be individually distinguished by peculiar specks on the body, were selected from about three hundred fish captured. By this means of selection, the possibility that the ten fish knew each other by sight was negligible. Morphological characters of these fish are listed in Table 1. An individual's

Table 1. Characters of fish introduced on August 11.

Individual name	Standard length (cm)	Body weight (g)	Release* of sperm	Sexual colour** pattern	Pearl** organ	Sex
A	12.5	34.0	+	++	++	male
B	9.1	13.4	+	+	+	male
C	8.4	9.8	+	+	+	male
D	8.6	11.4	+	+	+	male
E	8.2	10.1	+	+	+	male
F	10.2	19.7	−	+	−	female
G	8.3	10.9	−	−	−	female
H	10.1	18.0	−	+	−	female
I	8.3	12.4	−	+	−	female
J	7.4	8.1	−	−	−	female

* Release of sperm was checked by pushing the individual's belly (+, released; −, not released).

** Developments of sexual colour pattern or pearl organ were classified into three categories (++, well developed; +, developed; −, poorly developed).

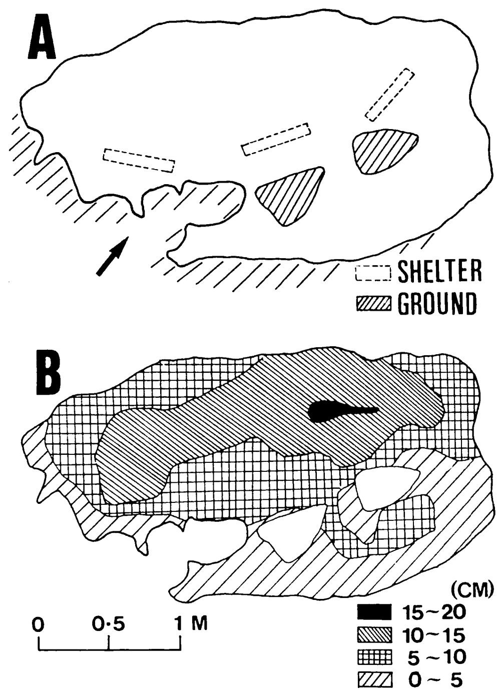

Fig. 1. Map (A) and distribution of water depths (B) of the enclosed pond. An arrow on the map indicates the direction in observations.

sex was determined by the colour pattern and presence of pearl organs or by the release of sperm.

Ten fish were then released into an enclosed part of a small pond in Kyoto University at 1: 30 p.m. (Fig. 1). The density of fish in the pond was 2.5 m^{-2}, which was within the limits of the natural densities of from 1.6 to 3.8 m^{-2} observed in the previous study (Katano, 1983). Three pieces of plastic tube, 40 cm in length and 8 cm in diameter, were placed in the pond to serve as shelters for the fish. Fish were observed from behind a vinyl blind situated about 50 cm from the pond edge.

Observations were conducted from August 11, when the fish were introduced, to August 30, when the fish became too inactive to be seen. Unfortunately, the fish were probably gradually preyed upon by birds and only five out of the ten introduced fish survived up to the end of the experiment. Individual B, which disappeared on the morning of August 12, is excluded from the results in this paper due to lack of aggressive interactions.

A maximum of three units of observation were conducted diurnally per day. In each unit of observation, the positions of individuals at the beginning and end of the unit were mapped, and all aggressive interactions during 30 minutes were recorded. The movements of individuals were also traced in order to describe the points where interactions took place and to record their feeding frequency. Beside these observations, some complementary interactions which were particularly intense and successive were also recorded.

Results

Aggressive behaviour. Behavioural patterns of *Z. temmincki* which were noted during aggressive encounters were as follows and are also illustrated in Fig. 2.

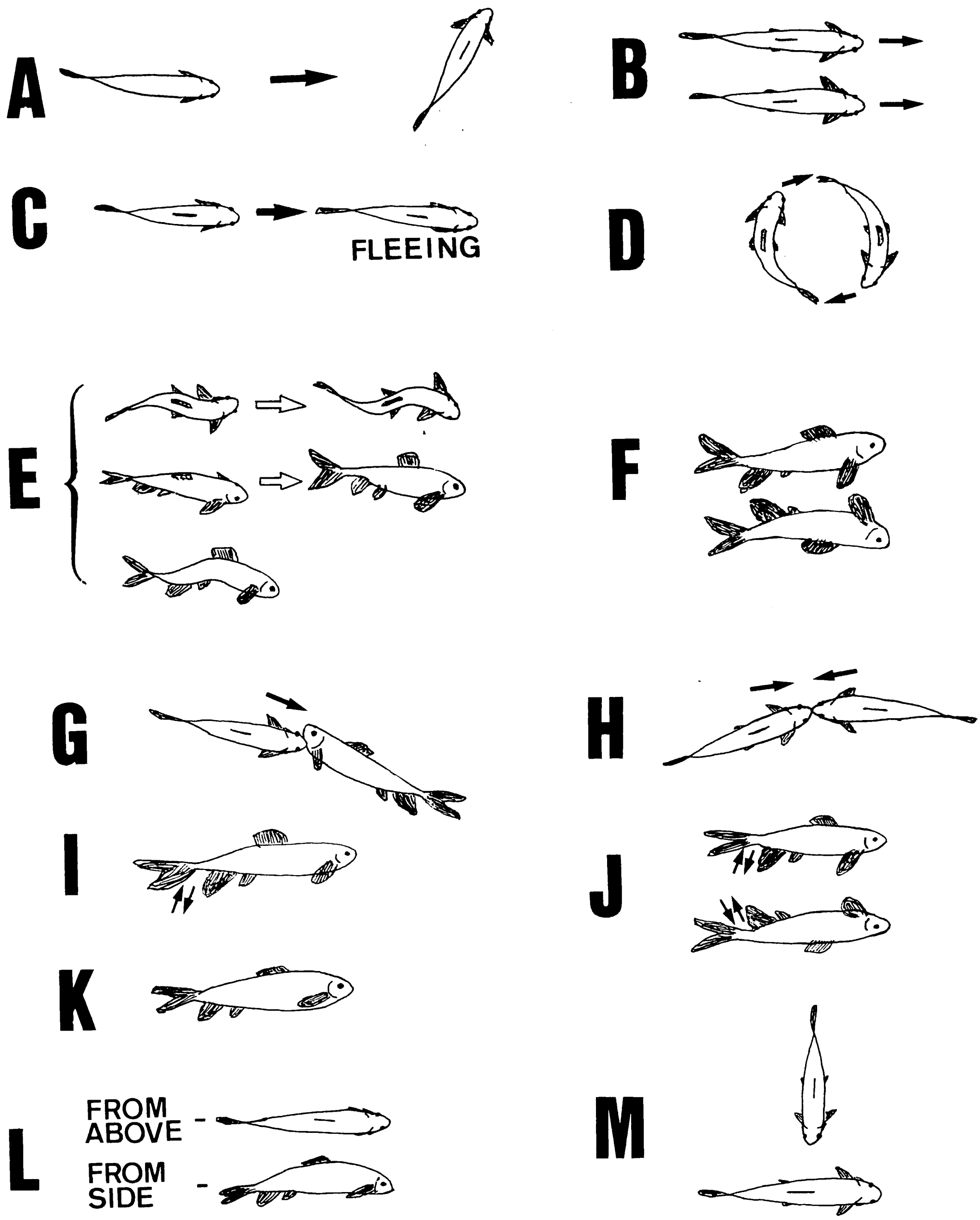

Fig. 2. Illustrations of the behavioural patterns of *Zacco temmincki* during its aggressive encounters (A, approach; B, parallel swim; C, chase; D, circling; E, lateral display; F, mutual lateral display; G, butt; H, mutual butt; I, tail beating; J, mutual tail beating; K, side-tilting; L, submission; M, standing posture). A black arrow indicates the direction of movement, while a white one indicates the sequence of the movements of the same individual.

Approach. The fish moves towards another fish.

Parallel swim. The two fish rapidly swim forward, parallel to each other. They often slowly diverge from each other while progressing.

Chase. The fish attacks or pursues a fleeing fish.

Fleeing. The fish rapidly swims away from the opponent.

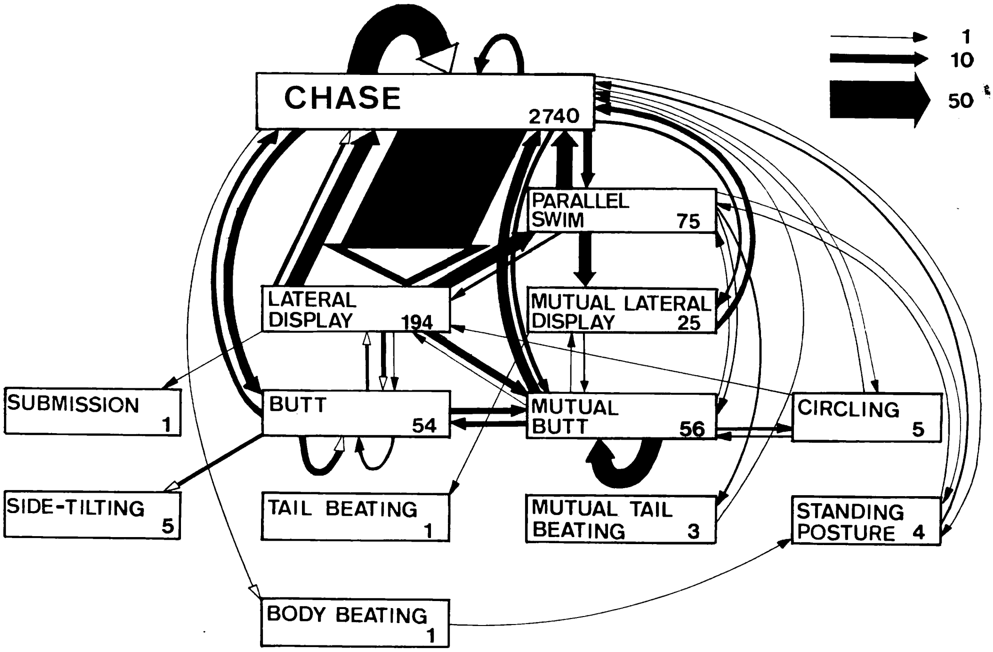

Fig. 3. Frequency and sequence of the behavioural patterns in aggressive encounters. Frequency of behavioural sequence is shown by line thickness. The white tip of an arrow shows the alternation of the performing individual, while a black one indicates the participation of at least one individual in both behavioural patterns.

Circling. The two fish pursue each other in a circle.

Lateral display. The fish presents the side of its body to the opponent. The entire body becomes rigid and all fins are maximally extended. There are some variations: i) a fish may bend the body into a S-curve with two bends, commonly to show its side to an opponent behind, ii) a fish may stand in place and incline the body laterally, usually to show its side to an opponent above, below or to the side of the displaying fish, iii) a fish may repeat the lateral movement described above while progressing slightly. Intermediates of these may also occur including both longitudinal and horizontal movements.

Mutual lateral display. The two fish perform lateral displays towards each other, frequently with their bellies adjacent.

Butt. The fish darts forward and hits the opponent with its head. Generally, the head of the opponent is butted, but while chasing the fish often butts the anterior part of the opponent. Sometimes the fish turns the opponent while butting.

Mutual butt. The two fish butt each other frontally.

Tail beating. One fish presents its side to another with its tail vibrating so as to direct beats towards the other.

Mutual tail beating. The two fish perform tail beating towards each other with their bellies adjacent.

Body beating. This is similar to tail beating, except the beating extends all over the body.

Side-tilting. The fish tilts it's body to the side with fins folded.

Submission. The fish folds its dorsal fin and collapses the caudal fin, and relaxes the entire body.

Standing posture. The two fish maintain a position, presumably threatening, one fish facing the lateral side of the other.

These behavioural patterns can be divided into either one-sided behaviour, or mutual behaviour in which the two participants behave similarly. In this study, the frequency and participants of the behavioural patterns were observed and counted, although approach was not recorded because it was very frequent and indistinguishable from chase.

Among the behavioural patterns mentioned above, side-tilting and submission along with fleeing did not seem to have an aggressive nature because the fins and entire body of the performer were folded and relaxed. They may therefore be considered as appeasement postures as noted in other species (Braddock, 1945; Chapman, 1962; Miller, 1964; Gibson, 1968; Gorlick, 1976), and hereafter will be excluded from aggressive acts. Aggressive fish occasionally darkened the entire body into deep grey, but it was not possible to quantitatively record the details of colour changes in this study.

The frequency of behavioural patterns and their mutual relationships are indicated in Fig. 3. Chase was observed most frequently. Parallel swim, lateral display and butt were common, while circling, tail beating, body beating, standing posture, side-tilting and submission were rare. The most common behavioural sequence observed was where chase led to the lateral display of the fleeing fish. Counter chases and repeated mutual butts were also seen frequently. Chase was usually observed solitarily, while the other behavioural patterns were often performed in connection with others.

The number of behavioural patterns in sequence is represented in Table 2. Successive behavioural patterns occasionally exceeded 10, in one case up to 107, although they were most commonly only one or two. These results are partly due to the fight on August 19 between individuals D and F, both of which became darkened. They performed 22, 107, 8, 14, 1, 1 and 5 successive behavioural patterns during short intervals over a twenty minute period. After 47 chases, 21 lateral displays, 3 parallel swims, 43 butts, 37 mutual butts, 5 circling and one mutual tail beating, this fight ended in individual D performing submission.

Table 3 shows the number of behavioural patterns performed by each individual. The frequency of

Table 2. Number of behavioural patterns in sequence.

Number of behavioural patterns	Number of cases
1	2,433
2	148
3	33
4	16
5	3
6	4
7	2
8	2
9	0
10	0
11	1
12	1
14	1
22	1
107	1

Table 3. Behavioural patterns of each individual during aggressive encounters.

Behavioural pattern	Individual										
	A	C	D	E	F	G	H	I	J	Unspecified	Total
Chase	15	1,075	476	404	429	112	62	98	26	43	2,740
Fleeing	0	72	156	259	367	390	478	438	537	43	2,740
Parallel swim	0	23	26	31	11	30	3	25	1	0	150
Circling	0	0	5	0	5	0	0	0	0	0	10
Lateral display	0	62	43	26	20	25	1	13	3	1	194
Mutual lateral display	0	5	6	9	2	15	1	12	0	0	50
Butt	0	4	15	2	30	0	0	2	1	0	54
Mutual butt	0	1	40	2	39	15	0	15	0	0	112
Tail beating	0	1	0	0	0	0	0	0	0	0	1
Mutual tail beating	0	0	2	1	1	1	0	1	0	0	6
Body beating	0	1	0	0	0	0	0	0	0	0	1
Standing posture	0	2	0	2	1	1	0	1	1	0	8
Side-tilting	0	0	0	0	0	3	1	1	0	0	5
Submission	0	0	1	0	0	0	0	0	0	0	1
Total	15	1,246	770	736	905	592	546	606	569	87	6,072

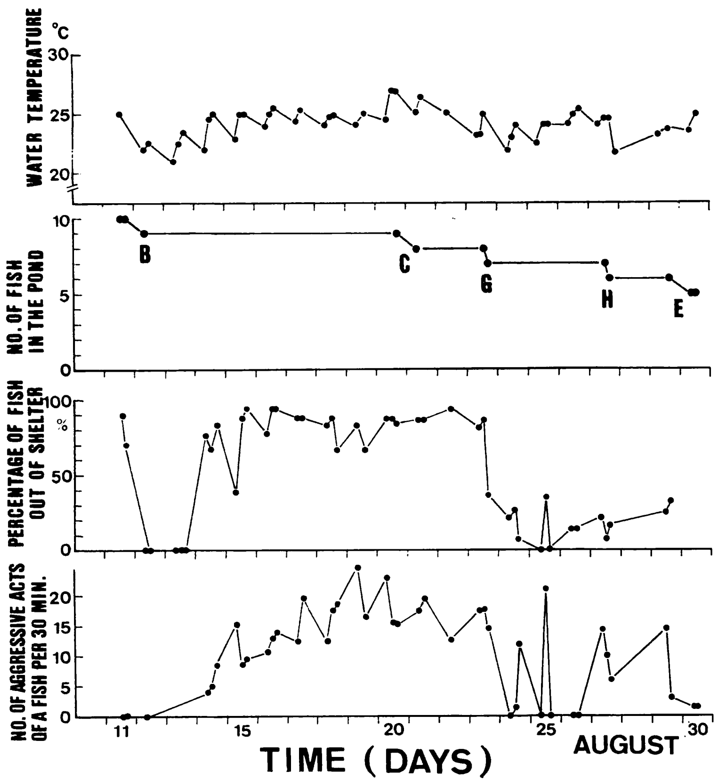

Fig. 4. Daily changes in water temperature, number of fish in the pond, percentage of fish out of shelter and number of aggressive acts for a fish per 30 minutes. Disappeared individuals are shown below the second graph. One mutual behaviour consists of two aggressive acts of each individual. The number of aggressive acts for a fish per 30 minutes was calculated by dividing the total number of aggressive acts by the number of fish out of the shelter.

chase and fleeing differed greatly among individuals. Side-tilting was observed only in females. Butt, mutual butt and circling were frequently performed by individuals D and F, reflecting the results of their fight. The other behavioural patterns among the other individuals were almost identical, except for individual A which performed only chase, and individual J which performed very few aggressive acts.

Daily changes in activities. Daily changes in water temperature, number of fish in the pond, percentage of fish out of the shelters and number of aggressive acts of a fish per 30 minutes are shown diagrammatically in Fig. 4. Although five fish disappeared one by one, the components of the pond were the same from August 12th to 20th. So far as appearance is concerned, the fish, which did not enter shelters when they were introduced, remained in shelters from August 12th to 13th. Then they came out of the shelters and began interacting frequently, about 15 times per 30 minutes for an individual. Such an active phase lasted until August 23rd when fish became inactive and showed few aggressive interactions. It is unknown why fish became inactive at the close of the experiment, but at least water temperature did not seem to have any influence.

Aggressive acts were divided into three types: i.e., chase, one-sided behaviour excluding chase, and mutual behaviour. The daily changes in the ratios of these three types in the total aggressive acts are indicated in Fig. 5. When the experiment was begun on August 11 only one chase was observed. On August 12th and 13th, when fish rarely came out of the shelters, mutual behavioural patterns such as parallel swim and mutual lateral display occupied all of aggressive acts. From August 14 to the end of the ex-

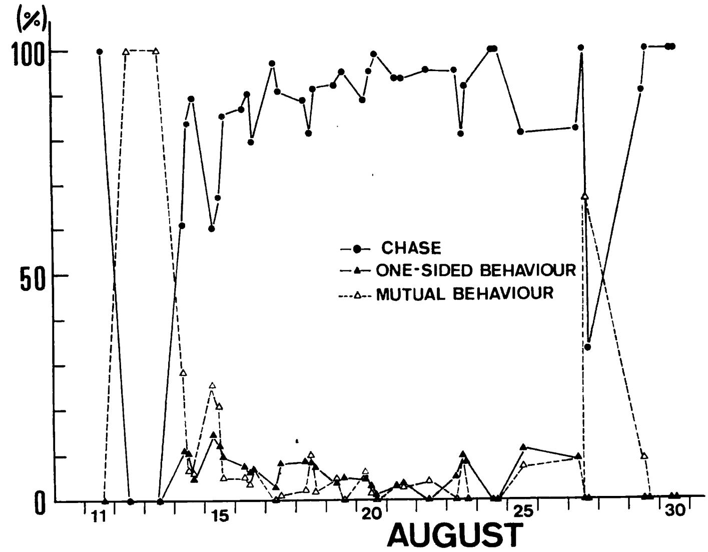

Fig. 5. Daily change in the ratio of chase, one-sided behaviour excluding chase, and mutual behaviour in the total aggressive acts.

Table 4. Dominance matrix during all observation periods.

Individual	Rank	Opponent								
		A	C	D	E	F	G	H	I	J
A	1		2	0	0	11	0	1	0	1
C	2	0		52	141	178	105	166	137	296
D	3	0	17		60	71	107	67	73	81
E	4	0	10	45		80	76	55	72	66
F	5	0	27	47	32		48	156	85	34
G	6	0	4	8	7	8		24	42	19
H	7	0	5	2	6	10	14		15	10
I	8	0	5	1	9	9	36	8		30
J	9	0	2	1	4	0	4	1	14	

periment, chase was most dominant, and both mutual behaviour and other one-sided behaviours were occasionally observed, except during one observation on August 27 when two parallel swims were recorded among six aggressive acts. Thus, mutual behaviour tended to occur more frequently during the early stages of the experiment.

Dominance relations. No universal measure of dominance has been adopted in studies on fish behaviour (Frey and Miller, 1972). In this study, when constructing a dominance matrix, I considered only chase-flee interactions because they were observed frequently and the winner was easily distinguished. The dominance matrix in this study including all chases is represented in Table 4. Individuals are arranged in a straight line without forming a circular relationship (e.g. A>B>C>A). Reverse attacks were occasionally seen, except against individual A, and constituted 12.5% (336 out of 2,740) of all chases.

To examine the daily changes in dominance, dominance-subordination relationships during each observation unit were divided into five categories and are shown in Fig. 6. Data on the dominance relationships of individual A are not given because only a few chases were recorded concerning this individual. In the early period of the experiment, many draws were seen reflecting the ob-

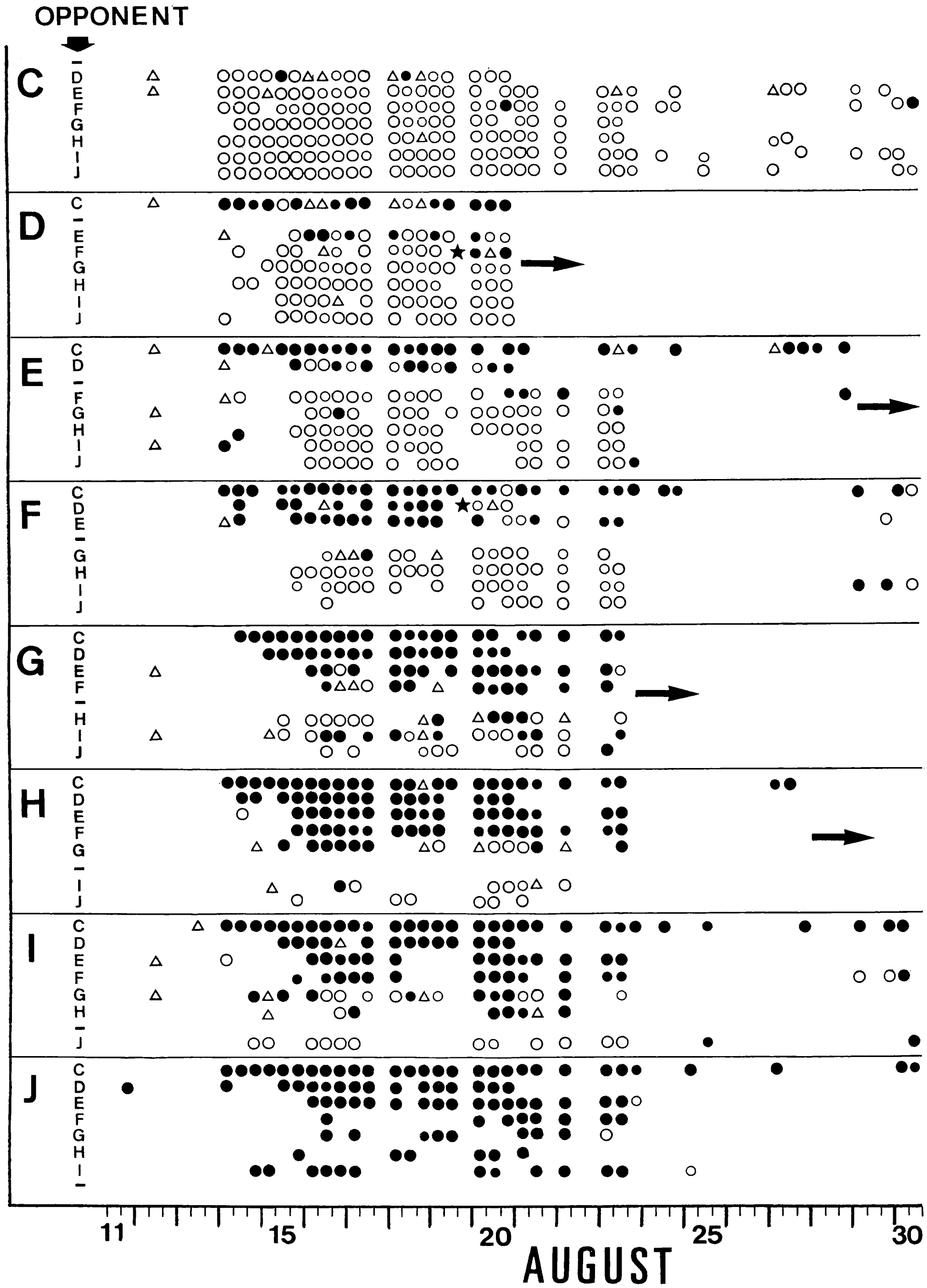

Fig. 6. Daily change in the dominance relationships in each observation unit. Three frames in one day represent three observation units. An arrow indicates the disappearance of an individual. A star mark, which is noted in the position of D–F relationships on August 19, indicates their fight mentioned in text. Dominance relationships were divided into five categories. ○, winning one-sidedly. ∘, number of wins exceeds that of losses. ●, losing one-sidedly. •, number of losses exceeds that of wins. △, equal numbers of wins and losses, or mutual behaviour.

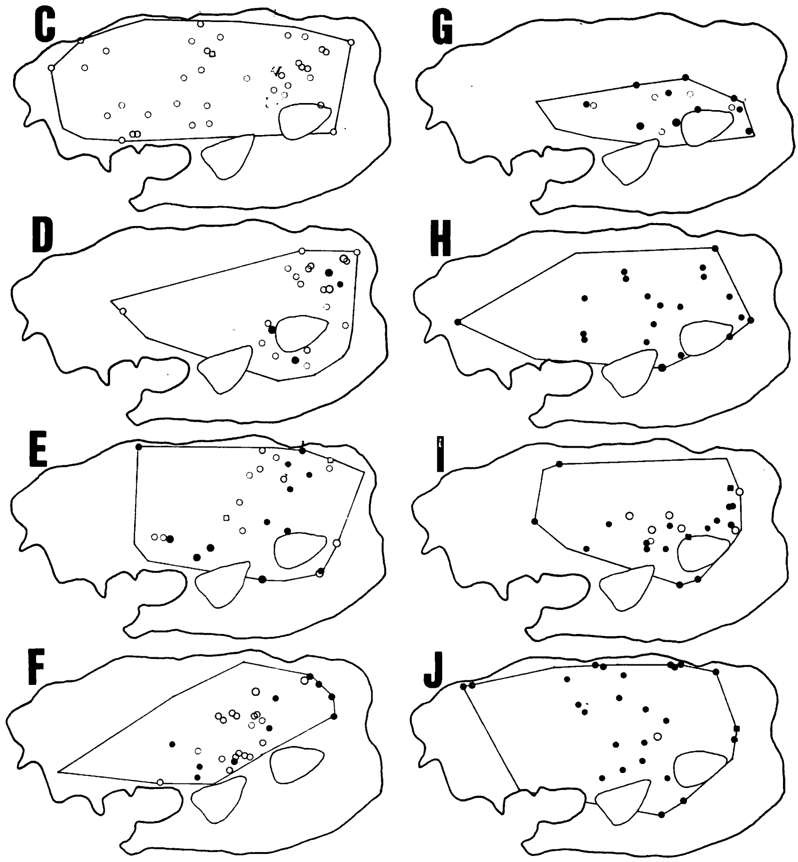

Fig. 7. Home range and distribution of chasing or fleeing points for each individual. Data are restricted to the period from August 12th to 20th, during which the components of the pond were the same. Home range was drawn by linking the outer points recorded either in the mapping censuses or in observations of aggressive interactions. Chasing (or fleeing) points for an individual are confined to the points where the individual began chasing (or fleeing). ○, chase of an individual in the higher rank. ◦, chase of an individual in the lower rank. □, chase of an individual which was not specified. •, fleeing from an individual in the higher rank. ●, fleeing from an individual in the lower rank. ■, fleeing from an individual which was not specified.

servation that only mutual behaviour was being performed at this time. Thereafter, one-sided dominance relationships constituted almost all interactions until the end of observations. Indeed, dominance relationships were stable between individuals whose ranks differed markedly, but they were unstable and occasionally upset between individuals in similar ranks. Such inversions of a dominance relationship were usually repeated many times.

The only example which showed a clear-cut inversion of a dominance relationship was observed between individuals D and F before, and after, their previously mentioned fight. Until the fight, individual D had been always dominant over F, but after the fight, which ended with the submission of D, their positions were clearly reversed. Furthermore, at times individual F also became dominant over C and E, over which F had never been dominant up until the fight.

In order to determine whether dominance depended on site or not, the home range and distributions of some chasing and fleeing points for each individual were recorded (Fig. 7). Although data are limited, the home ranges of individuals greatly overlapped and the distributions of chasing

Table 5. Feeding and appearance rate of each individual. Two kinds of feeding behaviour, snapping at a fallen object at the surface of water and sucking at benthic objects, were observed and counted. Appearance rate indicates the frequency of the fish coming out of shelter as obtained from 50 mapping censuses conducted from August 12 to 20, during which time the components in the pond were the same.

Individual name	Feeding rate/minute ( )=sample minutes Snapping	Sucking	Appearance rate
A	0	0 (6)	0.14
C	1.2	0.45 (22)	0.80
D	0.91	0.67 (21)	0.72
E	0.48	0.62 (21)	0.72
F	0.17	0.44 (18)	0.58
G	0.20	0.70 (20)	0.72
H	0.24	0.24 (17)	0.70
I	0.41	0.41 (22)	0.72
J	0.59	0.77 (22)	0.76

and fleeing points obviously indicate that they are not site-dependent for any individual.

In order to investigate the relationships between dominance and activities, feeding and appearance frequency of each individual are listed on Table 5. Two kinds of feeding behaviour, snapping at a fallen object at the surface of water and sucking at the bottom, were observed and counted. Although data on the feeding of individual A are insufficient, there is no correlation between dominance and feeding frequency in both feeding types (Kendall's rank correlation coefficient, $P>0.5$). Appearance frequency was similar among individuals excluding individual A which was quite nervous, and did not correlate with dominance (Kendall's rank correlation coefficient, $P>0.5$).

Individual recognition. When a fish was chased, it usually only fled, but in some cases it reacted to the opponent by performing lateral display, parallel swim or counter chase after fleeing a short distance. The mean distance of fleeing was 20.7 cm when the fish reacted in some way, which was significantly shorter than 63.2 cm when it only fled (t-test, $P<0.05$). Fig. 8 shows the frequencies of aggressive reactions to chasing. Opponents are arranged in order of dominance rank. Generally speaking, fishes rarely reacted against the dominants (20% at the most), though they reacted frequently, occasionally by counter chasing, against subordinates. Statistical analysis revealed that individuals C, D, E and I reacted significantly in accordance with the dominance rank of the opponent (Kendall's rank correlation coefficient, $P<0.1$, one-sided with samples more than 5), while others did not ($P>0.1$). Individuals H and J hardly reacted against any others, while individuals F and G reacted frequently against only one or two individuals. Such reaction types imply that fish generally recognized the relative hierarchical status of other individuals, although individuals H and J might not recognize any individual and individual F might recognize only H.

Two types of chase, one by the dominant and the other (reversals) by the subordinate were distinguished. Daily changes in the frequencies of the reactions to the two types of chases are shown with the ratio of reversals in Fig. 9. It is obvious that in every observation the reaction rates to the chases of the dominant were fairly low compared to those to the chases of the subordinate. Both rates, similar to the ratio of reversals, changed only slightly during the course of the experiment, about 5% and 50% respectively. These results imply that between August 14 and 29th individuals recognized the dominance of each other in the same manner.

Discussion

Examination of reversals. The ranking order of individuals was determined from the results of chases recorded during all observation periods. The dominance matrix was based upon peck-dominance because many reversals (subordinate attacks superior) were seen. Why reversals occur has been explained in some cases by site-dependent dominance (Brown, 1975), but in this study, individuals of *Z. temmincki* did not seem to win or lose owing to place. The frequency of reversals did not change significantly throughout the experiment. The number of aggressive acts per individual increased at the beginning of the experiment from August 12 roughly to August 17, but thereafter it remained at a similar high level until August 23rd. The decrease of aggressive acts in some observations after August 24th might be caused not by the stability in the dominance relationships, but by the inactivity of fish. Therefore, the occurrence of reversals cannot be attributed to any specific period when dominance relations were thrown into confusion.

Between individuals in similar dominance ranks,

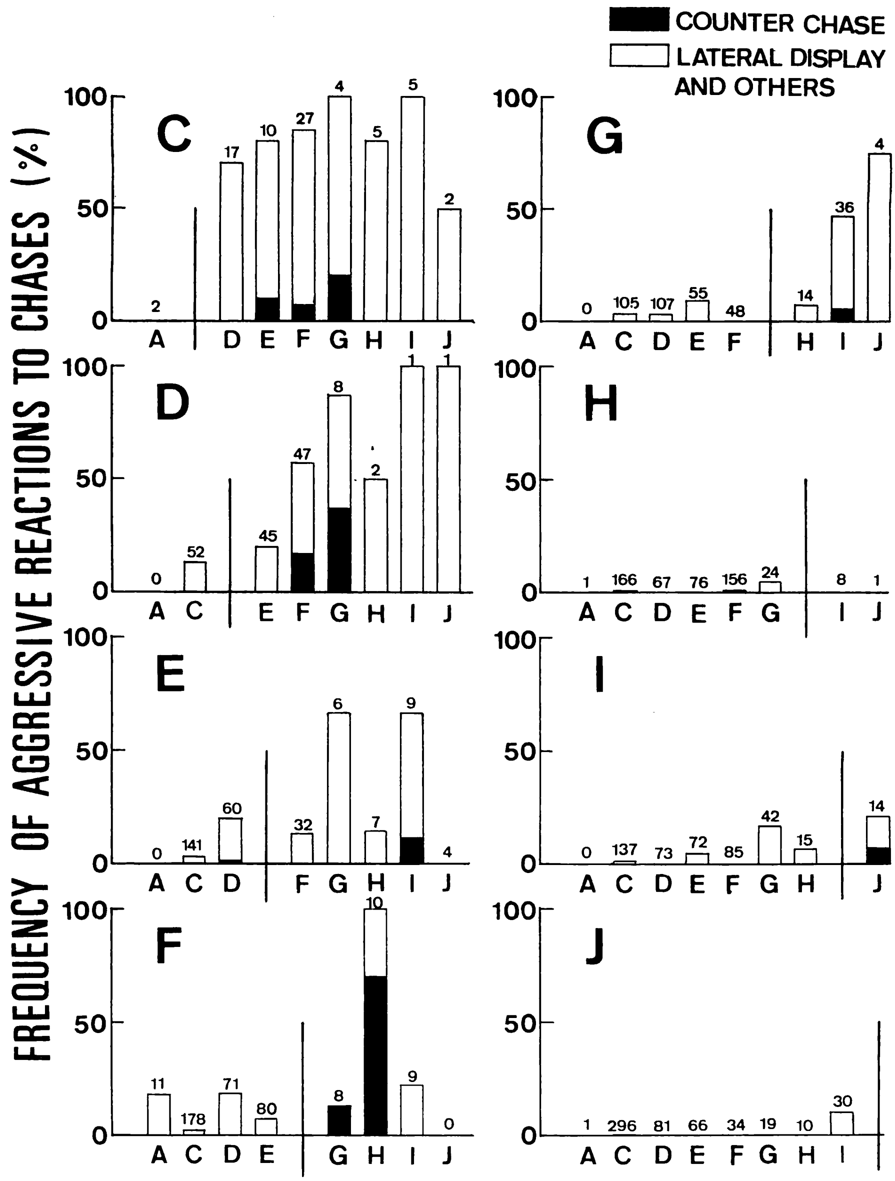

Fig. 8. Frequency of aggressive reactions to chasing. Data are given for each individual, and against each other individual which are shown in the horizontal axis in order of dominance. Data on individual A are deficient because it was never chased. A vertical line in the graph indicates the position of the individual in the dominance matrix. Figures on top of the graph represent the sample number.

not only were reverse attacks observed but also the dominance relationship itself was frequently reversed. Such inversions were not maintained in a stable state and were repeated many times. It is known that, in some fishes, the previous experience in winning makes the next aggressive encounter profitable (Braddock, 1945; McDonald *et al.*, 1968). Barnard and Burk (1979) called the hierarchy based on previous experience "confidence" hierarchy and mentioned that it might frequently change in stability with time. The example of individual F, which became dominant over indi-

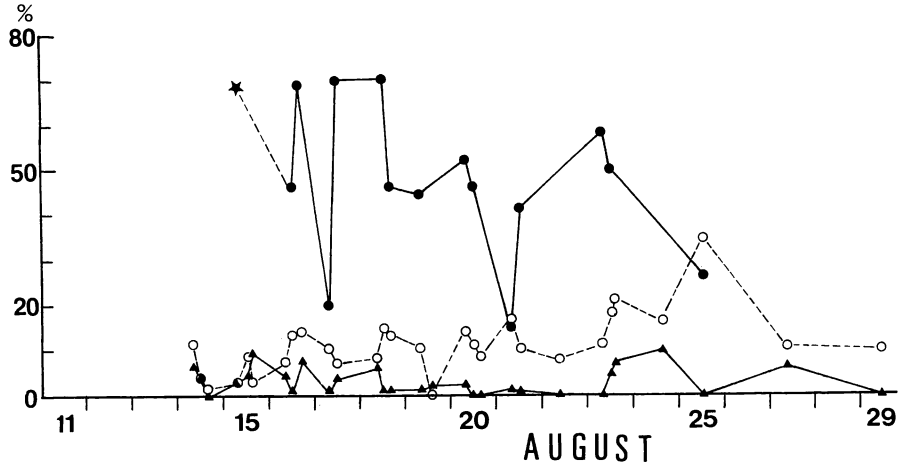

Fig. 9. Daily change in the frequency of reactions to chasing. Data are given when more than ten chases were recorded during each observation unit. A star mark indicates the reaction rate to 16 chases which were recorded from August 14 to 16. ○, chasing an individual in the higher dominance rank. ▲, reacting to a chaser in the higher dominance rank. ●, reacting to a chaser in the lower dominance rank.

viduals C and E after winning a fight with D, may imply the effect of previous experience on dominance. However, generally speaking, previous experience might not function in *Z. temmincki* because the dominance relationships of the fish were not stabilized despite the high frequency of aggressive interactions. Detailed analysis of aggressive encounters, including the mode of reaction to attacks, may be needed to explani the disorder in the dominance relationships of the fish.

Individual recognition. Individuals reacted to chasing in relation to the dominance rank of the chaser. This fact implies that the dominance order of the fish, as determined from the results of chasing only, constituted an important biological feature, and not merely an arbitrary observable behaviour. Generally speaking, it is probable for an individual to discriminate the dominance of the opponents depending on some kind of sign of their internal states without individual recognition. It is, however, unlikely that chased fish reacted merely according to the internal state of the opponent because every chasing fish seemed aggressive in the same manner. At first, I defined "individual recognition" as some kind of discrimination of an individual from other members in a group. It is unknown what kind of cues were used by *Z. temmincki* for the discrimination of an individual. They may only have responded to a relatively simple cue such as colour pattern. In any case, as Barnard and Burk (1979) point out, "there is no distinct division between assessment involving particular cues and so-called individual recognition". It may be concluded that individual recognition was certainly operative in the social interactions of the fish.

The means of reaction did not significantly correlate with the dominance rank of the opponent in some individuals although the reaction rate to the dominants was quite low in every case. Because they were the subordinates, individuals H and J rarely reacted to any other individual. Individual F reacted on every occasion against individual H with 80% of counter chases although with other individuals it only reacted to a maximum of 25%. Such a specific inter-individual relationship may be found variously if many individuals and situations are closely examined. Further investigations on individual recognition and its function in natural conditions will be needed in order to achieve a greater understanding of the social relationships of fishes. From August 14th, when chases became markedly frequent among total aggressive acts, to the end of observations, the reaction frequency to the attacks of the opponents did not change greatly. Considering that fish were captured separately, individual recognition among the fish seemed to be formed during the three days following introduction, when mutual behavioural patterns were dominant.

It remains unexplained why fish did not attack or react to attacks accurately in accordance with the dominance order in spite of their ability of individual recognition. The high frequency of aggressive encounters might cause some mistakes. Especially between individuals in similar dominance ranks, the dominance relationships were unstable and the response to chasing was varied. These results may show that individuals attacked or reacted to the attacks of the opponent against the dominance order although they did recognize the opponent. Individuals D and F fiercely fought on August 19 reacting successively to the aggressive acts of each other, which seemed to be an explosion of temper against a well known rival rather than random confusion.

Function of the dominance order. Why did the fish interact aggressively? Initially, competition for food should be considered since no reproductive behaviour was observed and males and females attacked each other. I had observed previously that under natural conditions males and females of the fish chased each other for food and space (Katano, unpublished). However, in this study, feeding frequency did not correlate significantly with dominance ranks. The food resources in the pond, such as drowned insects and benthos, seemed to be evenly distributed, and this means that dominance of the fish was not effective in gaining food.

I have reported that the dominance ranks of male *Z. temmincki* are effective in obtaining females during the reproductive season (Katano, 1983). The observation period in this study was within the spawning season of the fish in Kyoto city, from the beginning of June to the end of August. The rank order among males in this study might therefore be related to reproductive activities. The most dominant male, A, was not active and usually stayed in shelters. Male A had the most developed sexual characters and might therefore have been showing solitary behaviour prior to sexual activity. If some important objects such as a gravid female and a suitable feeding site are given, the dominance relationships of the fish would be clearly determined and would function effectively for a time, although they will sooner or later be reversed more drastically than they were in this study.

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カワムツの攻撃的出会いにおける個体認知

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野外の実験池において，カワムツの攻撃行動と順位関係について観察した．主な攻撃行動のパターンは，追い，側面誇示，平行泳ぎ及び頭突きであり，行動の連鎖としては，追われた個体が側面誇示をすることがもっとも多かった．実験初期には，二個体が互いに行なう側面誇示や平行泳ぎなどの相互的行動パターンが顕著であったが，実験開始後三日目からは追い行動がもっとも頻繁になった．観察された 2,740 回の追い行動の結果から，個体間には直線的な順位関係がみられた．しかし劣位者が優位者を攻撃することも 336 回観察され，それは特定の時期や場所に関わりなくみられた．追い行動とその後の行動パターンを分析したところ，追われた個体は追った個体の順位にほぼ応じて，逆に攻撃し返したり側面誇示をすることが明らかになった．この結果は，各個体が攻撃行動においてかなりの程度まで互いを認知することを意味する．このような個体認知は，相互的行動が顕著であった実験初期に形成され，また順位に反する攻撃のいくつかは，単なる誤りによるのではなく反逆の結果であるように思われる．

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