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Phylogeny of several motor patterns in fish investigated on the basis of the behavior of Haplochromis (Pisces, Cichlidae)

by Helmut Albrecht

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Phylogeny of several motor patterns in fish investigated on the basis of the behavior of Haplochromis (Pisces, Cichlidae)

by

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With three Figures

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Summary

The behavior of two mouth-breeding cichlid species, Haplochromis wingatii and H. burtoni, is described. Special attention was given to evidence for homology and homonomy in the analysis of the inventory of motor patterns. Almost all motor patterns typical for fighting behavior could be homologized with feeding or general locomotor patterns, or could be traced back to such patterns in cases where the form of the fighting pattern had been altered by specialization. The phylogenetically more recent motor patterns typical of intraspecific aggression depend on previously developed organs or motor patterns, for instance, jaws,

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teeth and biting behavior, and the motor patterns involved have retained the original autonomous motivation. For this reason, both feeding and fighting behavior exhibit motivational summation: Stimuli eliciting fighting promote feeding activity, and feeding, in turn, increases the motivation for fighting behavior, as has been demonstrated in quantitative experiments.

Similar relationships between feeding and fighting behavior are known in numerous teleosts, as is indicated by a comparative review. Recognition of the existence of motivational coupling, arising due to the fact that two drives at a high level of integration possess the same motor patterns as the common final pathway, provides a more simple explanation for behavior patterns previously described as displacement activities.

The behavior patterns employed in territorial defence are derived from feeding patterns and not from patterns typical of reproductive behavior.

Contrary to a widely held view, a large part of the behavior patterns observed in the spawning behavior of Haplochromis wingatii, H. burtoni and other mouth-breeders, which doubtlessly are descendants of pair-forming cichlids, can be traced back to fighting behavior patterns, and not the other way around. This is also true of other teleosts, in which the partners meet only for spawning, without prior pair formation.

A discussion is presented on the applicability of the concepts of homology and homonomy defined on the basis of certain criteria.

Acknowledgements - Professor Dr. K. Lorenz, my doctoral supervisor, led me already as student to the study of ethology. Later, he made it possible for me to carry out the present work at his Institute; I am greatly indebted to Dr. Lorenz for his generosity. Dr. [E.] Curio, Dr. [I.] Eibl-Eibesfeldt and Professor [B.] Hassenstein have assisted me in critical discussions of my studies.

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Relationships between fighting and spawning

Introduction and statement of the problem

While observing *Haplochromis wingatii*, a mouth-breeding cichlid from East-Africa, I was soon struck by detailed formal similarities between the motor patterns associated with spawning and those associated with fighting. Great formal similarities in entirely different functions represent a particularly important criterion of homology as well as of homonomy, and since the fighting patterns in question occur in similar form in many other fish groups distantly interrelated, there arose the question whether the motor patterns of spawning observed in *Haplochromis* could be traced back to fighting patterns.

That question hitherto had been raised in none of the numerous cichlids known. The investigations of the pair formation of these fishes (Seitz, 1943; Baerends, 1950; Oehlert, 1958) dealt chiefly with the behavioral patterns preventing fighting and binding the pair together. All these patterns play no role in the mouth-breeders coming together only during spawning.

The search for an answer to that question required exact comparisons of numerous motor patterns associated with different functional systems of behavior with the aid of criteria of homology (after Remane, 1952), which (according to Wickler, 1961) are valid not only for morphological characteristics but also for behavioral patterns.

That search led also to the question raised already by Wickler (1961), *viz.* whether and how motor patterns of fighting may be traced back to those of feeding. The main function of the present work is the elucidation of these two questions: Can the motor patterns of spawning be traced back to those of fight- 271
ing, and, in turn, can the motor patterns of fighting be traced back to those of feeding.

In order to elucidate these aspects, we must have knowledge of the behaviors of as many fishes as possible, for which reason we will, in the Sections on pages 291 ff. dealing with the alteration of functions of behavioral patterns, take into consideration also fish species other than Haplochromis.

Material and methods

Dr. Wickler has been kind enough to provide specimens of the East-African cichlids Haplochromis wingatii and H. burtoni for the purposes of the present study. These specimens were kept in aquariums of different sizes (50 to 5000 liters) at about 25 to 27°C. H. wingatii has been observed and bred since 1961, and H. burtoni, since 1962. The behavioral patterns have been recorded in writing and on film.

Criteria for homology

The phylogeny of behavioral patterns can be elucidated only on the basis of comparative research into specific characteristics, since evidence of paleontology is missing almost entirely in this field of science. Any reconstruction of this type of phylogenetic development stands or falls with the successful differentiation between homology and convergence.

Similar structures of common ancestry, i.e. homologous structures, according to Remane (1952), are established with the aid of the following methodical criteria. They all can be employed in an mutually independent manner, but yield no definite evidence, making homologies only probable. Homologization on the basis of only one of these criteria usually remains doubtful in character.

(1) Criterion of position - Relatively identical position within the system of patterns speaks for homology, but this only if the structures compared correspond in the number of elements to be homologized:

In most instances, we have not employed the first criterion; furthermore, Von de Wall's (1963) investigations have demonstrated that—at least in the case of the courting sequence of the Anatinae—sequences of definitely homologous elements may change very rapidly in the course of phylogeny, i.e. that the criterion of position is not reliable in this instance; there also arise difficulties, if the motor patterns to be compared exhibit different threshold values, so that the behavioral patterns cannot always be observed in their entirety.

(2) Criterion of special quality - Structures are more definitely homologous with increasing correspondence of special features, with increasing complexity of the special features, and with increasing degree of agreement. This criterion can be applied almost always, and functuons independent of the number of structural elements, but does not protect against confusion with analogies in cases where the function of the complex of features is either identical or unknown. The feature, thus, can never by itself give support except in cases where complete difference of function (page 297) can be demonstrated with certainty.

(3) Criterion of connection by intermediate forms - Even dissimilar or differently located structures can be homologized, of connecting transitory forms can be demonstrated—forms occupying positions that are taxonomically or ontogenetically located between the features being compared and, thus, meet the requirements of (1) and (2). Ethology, as a rule, is faced by more intermediate forms than morphology, since behavioral patterns vary even in the same animal depending on both intensity and function.

In some instances, viz. if homologies established on the basis of the second and first criteria do not fit in the case of the intermediate forms, the third criterion overrides the two other ones. 272

In addition to these three principal criteria, there exists a fourth one, viz. the distribution of a given feature. That criterion is of importance, in particular, in the following cases:

(1) Even simple structures are probably homologous, if they occur in a large number of closely related species, and this

(2) to an increasing extent, if these species exhibit additional similarities in similar distribution of structures, which, however, may not be correlated with the first structure regarding either function or ecology.

(3) Structures are not homologous with increasing probability with increasing occurrence in unrelated species.

This fourth criterion is of greater importance in the investigation of a relatively closely defined group of which very many forms are known, than in the investigation of general taxonomy of the zoological system.

Homonomy

On the basis of the criteria of homology, we are able to homologize also organs in one and the same organism, i.e. to establish so-called "serial homologies" (for instance, mouthparts, and walking-type legs in crayfish). They are called homonomies, since they are only indirectly of importance for the phylogenetic consideration of the organism; these factors are the products of the same genetic material, and phylogeny deals only with differences in genetic make-ups. Nevertheless, homonomies provide important intermediate stages within the framework of the third criterion of homology, in which connection it is assumed that nonuniform organs can be traced back to uniform ones——an assumption that, according to Remane (1952), is usually correct. Homonomies are very frequent in behavior, since identical motor patterns may be performed in connection with different functions.

Behavioral patterns

A. Marking patterns

The patterning of fishes belongs to behavior, and not only to morphology, to the extent that it is subject to physiological changes in coloration, i.e. is brought about by rapid migrations of chromatophores coordinated on a regional basis, which migrations are associated with certain behavioral motivations, i.e. moods as postulated by O. Heinroth.

1. Longitudinal and transverse stripings

(a) In other fishes - Like certain reptiles and mammals, numerous fishes possess cryptic striping; fishes existing chiefly in the open waters frequently exhibit longitudinal striping; those staying more or less motionless at a given site just as frequently exhibit transverse striping. Longley (1920), quoted after Wickler (1960), saw numerous coral fishes standing motionless at one location 273 showing transverse striping, but develop longitudinal striping once they started to swim about. Numerous marine species have moved, with time, from the rocky coast into the open waters, but have not fully lost their body patterning as, for instance, have the phylogenetically ancient pelagic fishes; their pattering has been transformed into longitudinal striping (Eibl-Eibesfeldt, 1962). Some coral fishes (for instance, *Eques acuminatus*) exhibit a similar change even still in their ontogenesis. Only the fish swimming at an angle with the head up (*Poecilobryon* [*Nanobryon*] *eques* STEIND.) stand during the day motionlessly in the water, but still exhibit longitudinal striping. However, the longitudinal axis of that fish is very steep, i.e. inclined by about 44 to 72 degrees with respect to the horizontal. With onset of dusk, this fish adopts a less steep position (inclined only 11 to 42 degrees), the longitudinal stripe disappears, and the

fish exhibits transverse striping, which becomes more distinct with increasing approximation of the horizontal position (Braemer, 1958). Badis badis shows transverse stripes during threatening, and this ontogenetically for the first time when establishing the first territory (Barlow, 1962).

In the latter instance, we then find that the appearance of transverse striping is associated with a certain motivation. In cichlids, transverse stripes may appear not only during territoriality (aggression), but also during camouflaging (fear), and this at different parts of the body.

In Tilapia species, transverse striping is in evidence, during escape motivation, chiefly on the body; during aggression, chiefly on the head. Tilapia mossambica exhibits transverse stripes during boundary fights and in courting dress (Oehlert, 1958) and during fear, i.e. when it is trying to conceal itself (Baerends, 1950). In numerous Tilapia species, in which the sixth chromatophore system (Barends, 1950) covers the remaining body patterns, there remains only the transverse stripe at the eye, and advertises intention to attack. That facial pattern, as I call it in Haplochromis, has been transformed into a signal in many species (cf., for instance, Peters, 1937).

Pelmatochromis guentheri leading young exhibit transverse stripes, if they remain at one location for a relatively long period of time. The intensity of their attacks at that location increased with increasing darkness of the transverse stripes. In the cichlids, too, we find that the young of species moving about in the open waters exhibit longitudinal stripes, while those living more under cover exhibit transverse stripes (Albrecht, 1963).

(b) In Haplochromis - Depending on momentary motivation, both H. wingatii and H. burtoni are able rather rapidly to change their patterning, which—like that of H. desfontainesii (Kirchshofer, 1963)—consists of both longitudinal and transverse stripes. All exhibit (1) dark transverse stripes during camouflaging and during attack, (2) two longitudinal stripes in fear situations (= escape), and (3) a transverse stripe at the eye during aggressive behavior and during acquisition of territory. (1) plus (2) and (1) plus (3) may also be seen simultaneously. Longitudinal and transverse stripes can be seen simultaneously when the fish has fled to a protected spot (cf. also Myrberg, in the press; and Heiligenberg, 1964).

During attack, the transverse stripes on the flanks reach further down than during camouflaging (cf. co-shading, p. 274). Morphologically, the patterns of markings exhibited by *H. wingatii* and *H. burtoni* resemble those exhibited by *H. desfontainesii*, and they have the same functions and are reflections of the same motivations. With the aid of the first three criteria, they can be homologized with certainty. In cichlids we are generally able to employ criteria (1), (2) and (4).

The following observations show that the transverse stripes are "recognized" also by the companion as postulated by K. Lorenz—represented, in the present case, by the mother. A *H. wingatii* female guarding her young hardly pays attention to young of her own species, but she constantly chased *Cichlasoma nigrofasciatum* of about the same size, which were swimming in the swarm, and would even kill them, in particular, at the center of her territory.

These fishes did not lose their transverse stripes, when they were chased, 274
i.e. they constantly stimulated the female to attack; this is in contrast to the *Haplochromis* young, which were chased only, when they became territorial for brief periods of time, and then exhibited transverse striping.

On the basis of these observations, we are permitted to conclude that resident (or territorial) individuals are not tolerated in the vicinity of an

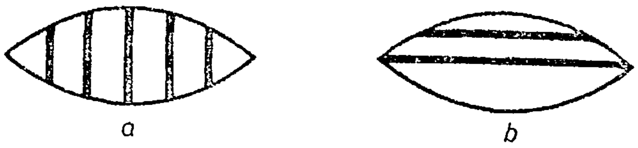

Figure 1 - The models used were pieces of cardboard of the sizes shown; they were presented to the fish outside of the aquarium on a long, thin stick.

established territory. In order to determine whether behavioral differences might play a role in this connection, I presented two models with transverse stripes and longitudinal ones, respectively, to females having young of the same age (Figure 1).

The dummy with transverse stripes elicited attack in an aggressive female; on presentation immediately afterwards of the dummy with the longitudinal stripes, that female swam briefly toward the dummy and then turned away. The other female was timid. She paid little attention to the dummy with longitudinal stripes, but followed the one with transverse stripes with more interest.

If Haplochromis responded to different scents similarly well as Hemichromis does according to Kuehne (1963), that would then explain the relatively weak response of Haplochromis to these dummies. As long as the young Haplochromis are schoolers (Albrecht, 1963), they exhibit transverse striping, but only an indistinct one, which apparently does not upset the mother.

Haplochromis, thus, exhibits transverse stripes only when it stays at a given site, bu it due to fear or due to territorial motivation; only territorial fish will attack other individuals.

2. Co-shading

In some cichlids (for instance, Cichlasoma facetum, C. nigrofasciatum, and Nannacara anomala), the transverse asexual cryptic patterning turns into the contrasting pattern of the conspicuous courting dress (Seitz, 1949). The situation is identical in *H. wingatii* and *H. burtoni*. In addition, in all these five species, the upperside turned toward the light becomes light, and the underside becomes dark, and, furthermore, the transverse stripes reach down further than in the cryptic dress. This co-shading enhances the contrast produced by light and body-shadow, i.e. the body provides a more plastic impression (Albrecht, 1962).

On the other hand, counter-shading widely found in the piscine kingdom (Sueffert, 1938) has a camouflaging effect, where the side turned toward the light is dark, and the underside, in the shadow, is light. The fish, thus, acquires a "non-objective" appearance.

Each object is more or less conspicuous within its environment. For a given animal, each situation—being more conspicuous or being less conspicuous—has its own advantages. Contrasting coloration, in general, has a signal function and this, in particular, in threat displays; cryptic coloration conceals the animal from its predators, and the predator from its prey. In this connection, it depends on the environment what actually will be conspicuous (1) as little as possible or (2) as greatly as possible. Two types can be distinguished: Animals are making use (a) of light-versus-dark shadings in visually uniform environments, 275 and (b) of manifold patterns of spots in visually well divided environments. Of decisive importance in this connection is the size of the animal compared to the environmental pattern. Examples: Re. (1a), herring; (1b), flounder; (2a), *Haplochromis* male; and (2b), coral fishes.

B. Relationships between feeding and fighting

(a) In other fishes - Wickler (1961) has drawn attention to certain relationships between feeding and fighting, and, from the point of view of

phylogeny, he interpreted numerous threat patterns as motor patterns associated with feeding: "The function, in the service of which a given behavioral pattern is usually exhibited, is regarded as the most ancestral one, in particular, if it, in functional terms, is correlated with other features, which are also specialized in the service of that function. Numerous animals, for instance, threaten with opened mouth; that motor pattern, no doubt, originally had a function in taking in food, just like the mouth, the gastro-intestinal tract, etc., have evolved in the service of that function" (Remane, 1952).

I am presenting here only a few examples for fishes; for additional ones, cf. Wickler (1961). All examples show not only that the motor patterns associated with feeding and those associated with fighting are similar, but also that the internal motivations have common features. These examples have not been selected at random. Among all the papers available to me, I have found none indicating that feeding can be related in a similar manner to other behavioral patterns.

Kalleberg (1958) has compared the motor patterns of feeding with those of threatening in salmonids: Fighting behavior appeared in young salmonids only after they had started to feed. The extraordinary resemblance between the frontal threatening exhibited by salmon and trout broods and the posture exhibited by the fish approaching a prey animal suggests that that frontal threatening consists chiefly of elements associated with feeding behavior. Before the prey is finally seized, we may frequently see a conflict between "approaching" and "swimming away" (= threatening).

In both Salvelinus fontinalis and S. gairdneri, aggressivity increases with feeding (Newman, 1956). In individual fish observed for well over a week, the number of attacks on other individuals increased after meals, and this from 394 to 846 in S. gairdneri, and from 324 to 833 in S. fontinalis.

Salmo alpinus shakes prey that is too large, and snaps at it; similar motor patterns appear during fighting (Fabricius, 1953) (who, in my view, has described these patterns incorrectly as "displacement movements," cf. page 294). Fishes establishing a territory swim about as if foraging (Fabricius, 1953; 1954). Galaxiids (*Aplocheilus*, *Panchax*) snap during sexual fighting just like they snap at prey (Lorenz, personal communication).

When one stickleback happens to find a titbit, and starts to devour it, others rush toward it and try to rob it (Tinbergen, 1955). The feeding posture with the head pointing toward the bottom is a signal, which "attracts all other members of the school to the source of food" (Keenlcyside, 1955). It is not clear what is meant by "attracting" ("Ziehen"). Sticklebacks actually raise their spines more steeply with increasing size of the titbit, and they do that also during fighting. The posture with the head pointing down also represents a threat posture. Aggressively motivated, these fish then swim toward the food item; occasionally, they flee just before reaching the food, and feed only on their next approach.

Esocid females not ready to spawn and escocid females having almost completed spawning drive approaching males away with a shaking of the head—an element they exhibit also when facing large items of food: The head beats to 276
one side a returns again to the median line (cf. Fabricius, Film, 1958). Wickler (personal communication) has observed juvenile pikes, which, when facing either opponents or large prey animals, bent their vertebral column in a kyphotic manner, lowered the branchio-stegal membrane, and spread the paired fins.

Badis badis frequently feeds during breaks in fighting (Barlow, 1962). Species belonging to the genus *Etheostoma* become particularly aggressive when they are being fed (Winn, 1958).

In swarms of Tilapia natalensis fighting takes place only during, and right after, feeding (Baerends, 1950).

In Pelmatochromis, aggression is most intensive after feeding; ontogenetically, defense of a territory occurs for the first time after a feeding session (Myrberg, in the press); fishes feeding on algae, which remove that food from substrates overgrown with algae by rapid scraping movements—like Labeo bicolor, Homaloptera, and Gastromycon—swim side by side during fighting, forcefully scraping the substrate or even the open water (Labeo) (Wickler, 1961). Helostoma temminckii licks its mouth during fighting; Tropheus duboisi scraps the flanks of its fighting partner (Albrecht, 1962). According to Wickler (unpublished results) the specialized motor repertoire of feeding supplies in these cases the "raw material" for the motor patterns of fighting.

(b) Relationships between feeding and fighting in Haplochromis - When juvenile Haplochromis search the sand with their mouths for something edible, they acquire transverse stripes and start fighting, and this also when no food is present.

Using about fifty H. burtoni individuals, three to four weeks old and measuring 1.5 cm in length, I determined the intensity of aggressivity on the basis of the number of attacks. These fish were kept in an aquarium known to them. Stimuli eliciting flight were avoided, since, according to Noble and Curtis (1939), unknown environments enhance schooling behavior, and, according to Heiligenberg (1963), schooling behavior and aggressive behavior are negatively correlated in Pelmatochromis kribensis. My experimental animals did not swim about in a school, but were distributed loosely over the aquarium. They did not yet exhibit territorial behavior. Since, first, aggressive behavior and territorial behavior are positively correlated, and, secondly, no additional behavioral motivations are coupled with either feeding or fighting at that age, the

Table 1 - Number of attacks (nA) and of biting attempts (nB) in about 50 H. burtoni at 'more', or 'less,' than eight cm above the bottom 'before' and 'after' feeding

	nA	nB	
before	-	-	more
	6	11	less
after	23	46	more
	256	566	less

relationships between feeding and fighting are clearly reflected in this experiment. In these small fish I was unable to observe well any appearance of the eye stripes. Since each attack differed in intensity, I determined also the number of biting attempts per attack (Table 1).

The fish were far more aggressive at the bottom, although both the Artemia nauplia and the fish themselves were uniformly distributed over the water space, measuring 35 cm in depth. This corresponds exactly to the preference of the bottom for establishing territories to be discussed in detail on pages 279 and 284.

Older individuals pursuing a prey animal acquire a facial pattern and, 277
in between, attack individuals of their own species at the feeding site. Under the latter conditions, even females will attack males, which they never do under other conditions, since the males are bigger and stronger. The fish swim very rapidly toward the sinking titbits "with hand-brake set," i.e. with pectoral fins beating in the forward direction, snap up the titbit, and return with a vigorous tail beat (a fighting movement) (cf. p. 286, in that connection); next, they usually acquire their facial pattern.

A Tilapia galilaea male defended his spawning site only when another male dared to feed at the bottom, although there were no edibles there. The intruder acquired an eye stripe before he went down to the bottom to feed. (*Tilapia galilaea*, like most tilapias, exhibits that stripe also during fighting.) That sequence was repeated numerous times. The fish, then, demonstrates his aggression by feeding, and the partner responds logically by counter-attacking.

All these examples show that the motivation to feed or the efficiency of the stimuli eliciting that motivation, respectively, is enhanced in a demonstrable manner by aggressive motivation and *vice versa*, that the motivation to fight is enhanced by motivation to feed.

Teleosts are the lowest vertebrates, in which intraspecific aggression occurs and begins to unfold its doubtlessly important survival function, *viz.* distribution of the individuals over the space. Aggression is hitherto not known from among the elasmobranchs. In the ancestral series of the chordates, capture and consumption of relatively large prey animals apparently have appeared relatively late; all early forms and, at the present time, still some larvae—like ammocoetes—are whirlers. The toothed mouth in the service of food intake, no doubt, is phylogenetically very much older than intraspecific aggression, which, in the ancestral series of the pisces, appears probably for the first time in the lower bony fish *Amia calva*: The male constructs a nest for the brood and defends that nest.

In this way, the organs and motor patterns of feeding have acquired their additional function, *viz.* to attack conspecific individuals. That is valid in a very general way: More, for instance, in the case of canid predators than in that of fish. In the Canidae, as is well known, the motor pattern of firmly seizing and shaking in fighting is identical with that in killing prey.

All motor patterns described so far are patterns that are largely identical in their forms during feeding and duting fighting. The bending of the vertebral column and the spreading of the fins in the pike indicate, with certainty, a conflict between swimming forward and swimming backward (= threatening; cf. also further above in that connection: Kalleberg, salmonids). In this way, the prey is watched and not prematurely chased away. The spreading of the gill covers [actually: raising of the gill covers], with certainty, can be attributed to the increase in respiration during aggressive activity. This raising of the gill covers has a function primarily in enlarging the oral space for 'inhaling' the prey. The visual epiphenomenon—enlargement of the body outline—has an intimidating effect and, as secondary function, exerts a selective pressure in the direction of differentiation to the threat gesture. The gill covers then are frequently colored and are adorned with eye spots. Finally, the cottids and the pomacanthids have added spines to their gill covers for defense.

In the animal, aggression and hunger, in addition to escape and sexual drive, represent the most general sources of drive we know. However, it has been known for a long time that not only each "major drive," but actually each individual instinctive movement possesses its own autonomic motivation, which gives 278 rise to a particular appetitive behavior directed at that motivation (Lorenz, 1935). That is valid even in the case of simple coordinations of movements, like swimming, running, and gnawing [Lorenz' (1935) tool activities]. However, if each such tool activity possesses its own motivation, then there arises a mutuality of the motivation of all so-called major drives, in which they (as common final pathway, as postulated by P. Weiss) are used in the same manner. As has been demonstrated by Heiligenberg (1963) in Pelmatochromis kribensis, the readiness to flee and to form schools is significantly greater if, by chance, the motivation (readiness) for locomotion is high at that moment. An analogous relationship is found in the motor patterns of feeding in the fishes observed by me between the motivations for feeding and for fighting, in which they are employed in an identical manner.

In phylogeny, thus, the aggresive drive has taken over the motor patterns of feeding, and now feeding frequently is associated with aggressive motivation.

Evolution proceeds in an "opportunistic" manner, in that it makes use of available elements for the solution of new problems. To fight with the motor patterns of feeding was a "particularly obvious" step.

In literature we find very frequently the term "displacement feeding" for feeding during breaks in fighting. It is more simple to interpret that activity as newly orientated movement (Tinbergen, 1960), as seen for the first time by Grzimek (1944) in the case of the so-called "bicyclist response" (Radfahrer-Reaktion: To avoid the higher ranking individual, and to threaten or peck the lower ranking one; Translator]. In these cases, the aggressive response elicited by a certain object, but at the same time inhibited by the escape drive, is directed toward a less fear-inducing object. Even more simple is the interpretation offered by Wickler (1955), who was able to demonstrate that the performance of a partial activity of an Instinct A, which is a partial activity of Instinct B, may facilitate the latter one. Exactly this relationship exists between the behavioral patterns of fighting and of feeding in the Haplochromis species investigated and, probably, also in many other species, as demonstrated by the above-presented review of the literature.

The instinctive movement associated with aggression, thus, is not suppressed and replaced in an allochthonous manner by the movement of an uninvolved drive as displacement movement as postulated by Tinbergen (1940), but is only directed toward an uninvolved object.

Only in exceptional cases, aggression makes use of weapons evolved under selective pressure for defense against predators; thus, probably the horns of bovines and, without doubt, the sharp dorsal spines of certain percomorphs.

Their primary function is to make swallowing difficult for the predator (cf., for instance, Hoogland, Morris and Tinbergen, 1957); the same is valid, without doubt, in the case of the dorsal and abdominal fins of plectognaths. The employment of these defensive weapons also in intraspecific fighting appears so obvious that some observers have been fooled by their imagination. For instance, the New Brehm (p. 349) still states that sticklebacks attack each other with their spines so forcefully "that the one partner sinks pierced to the bottom."

Actually, we know hitherto only in the case of the chaetodontids that their spines are used in intraspecific fighting.

Two specialized forms (Chelmon rostratus and Heniochus acuminatus) have evolved highly ritualized forms of fighting (Zumpe, 1962; 1963).

(C) Territorial behavior 279

(1) of the Haplochromis male

(a) Acquisition of territory and colony formation - A male swarm member gradually acquiring territorial motivation first loses the longitudinal stripes and swims about less than the other members of the swarm. Gradually there appear transverse stripes along the flanks, which stripes become more distinct on the upper parts with prolonged possession of the territory. There are two stripes on the forehead between the eyes; the lower one continues on into the longitudinal stripe of the body; the upper one crosses the gill covers. One stripe passes vertically through the eye and continues at an angle to the corner of the mouth. The facial pattern (cf. p. 273) consists then of two transverse stripes and one longitudinal stripe. The underside of the body becomes deep black; the back becomes grey; the dorsal fin becomes metallic light blue (co-shading, cf. page 274, and Albrecht, 1962). That pattern is exhibited as long as the male retains its territory (cf. Figure 1a).

The individual male always touches the bottom at a certain site and resists attacks by other males only at that site. Up to five males may become territorial within an aquarium having a floor space of 80 x 150 cm.

I have observed the first occurrence of territorial behavior in Haplochromis juveniles in connection with feeding, mouthing of sand, and digging. These three activities can be homologized in accordance with the second and third criteria.

Heiligenberg (1963) has been able to demonstrate in Pelmatochromis kribensis that the level of aggressive motivation determines the extent to which feeding movements are transformed into digging movements.

The fish start to become aggressive during feeding, complete the aforedescribed change in coloration, and, at least at the feeding site, behave exactly like territorial males. This process can be initiate with the fish initially feeding in vacuum.

When adult individuals establish a territory, they usually leave out both feeding and mouthing of sand, and immediately start with digging. In their natural habitat, feeding and fighting, no doubt, play a similar role in the facilitation of territorial behavior.

Kirchshofer (1953) observed Haplochromis desfontainesii males in their natural habitat together in colonies. Each member of the colony possessed its defined territory, which, depending on the character of the substrate, measured 0.5 to 2 m in diameter.

In an aquarium measuring 1.80 x 1.80 m, I was able also in H. wingatii to observe the onset of colony formation. The territories had diameters of between 20 cm and 1 m, with a pit at the center; the territories were arranged close together, although there was enough room for avoidance.

It is probably their schooling or swarming behavior, which enable these fishes to establish territories close together. Baerends spoke in this connection of a territorial society, and Kalela (1954) of solidified swarms.

(b) Territorial behavior (apart from fighting) - In *Hemihaplochromis multicolor*[1], Reinboth (1956) did not wish to regard the pit as the center of the territory, because fighting did not occur there at a greater rate. 280 He has confused in that connection the frequency of fighting with the intensity of fighting motivation; the pit most definitely is the center of the territory.

¶ In *H. wingatii* and *H. burtoni*, as probably in all territorial animals, fighting occurs most frequently along the boundary of the territory. "Territories are determined not by rigid geographical boundaries, but rather by the fact that the fighting motivation of the animal in question is maximal at the site best known to it, *viz.* the center of the territory; or expressed differently, at the site where the animal "feels most secure," i.e. where its aggression is least suppressed by escape motivation. With increasing distance from its "head quarters," motivation to fight decreases to the same extent as the environment becomes more foreign and intimidating for the animal (Lorenz, 1963).

At the common territorial boundary of *Haplochromis*, fighting drive and escape drive are almost balanced, and fights therefore occur most frequently along that line.

By means of continuous digging along the rim of the pit and pendular "swimming-at-the-spot" the fish moves the central "threshing floor" up to ten cm deep

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[1] For this fish, which has previously been counted with the genus *Haplochromis*, Wickler (1963) has erected the new genus *Hemihaplochromis*, since it occupies a position between *Hemichromis* and *Haplochromis*. *H. strigigena*, now *Hemihaplochromis* species, also belongs to that new genus, since the real *Haplochromis strigigena* was not investigated by Seitz (1942).

into the sand, so that a crater with an even floor is formed. All pebbles, having at least the size of Haplochromis eggs, are carried away by the male. If a large pebble remains at the rim of the pit, we find that the threshing floor may be tilted in that direction, since the sand is removed from there just as frequently as from the other sites, but does not slide down along the slope.

The eveness of the threshing floor may facilitate the rapid pick-up of the eggs freshly deposited into the pit (cf. p. 290). The eggs are not equipped with adhesive threads, as those of most cichlids (Wickler, 1962), and would easily roll away from a purely funnel-shaped nest hole, as found in the majority of cichlids.

Shifting of the pit due to digging in one direction or sudden changes of territory do occur, i.e. territorial tenacity is not absolute (Figure 2).

If floating plants are removed from the aquarium, the individuals will increase their courting displays and will fight more along the territorial boundaries. In the natural habitat, the colonies probably would be located at well illuminated sites (cf. Albrecht, 1963). On illumination of the aquarium, juveniles swim into the open water and start to dig and fight. In the natural habitat Kirchshofer (1953) also found colonies of Haplochromis desfonatinesii at strongly illuminated sites, as did Lowe (1956) in the case of Tilapia karomo.

During possession of a territory, the dorsal, anal and abdominal fins of the males grow in length, independent of both age and size of the individual; in males prevented artificially from establishing a territory, the fins remain as short as those of the females.

Males establish territories also in the absence of females.

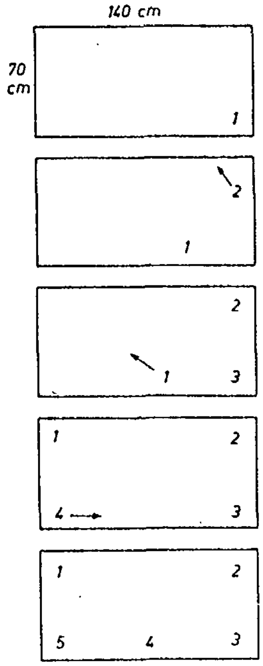

Figure 2 - Outline of an aquarium with numbered territories

(c) Discussion of the roots and functions of territorial behavior - According to Tinbergen (1952) a territory is an area, that is defended by the fighting owner shortly before, and during, the period of breeding. Thus, at least two animals are required. According to Baerends (1950), territorial behavior in cichlids is subject to the reproductive drive. Thorpe (1956) has regarded territoriality in fish outside of the period of reproduction as particular exceptions. 281

According to Wickler (1958), typical reproductive behavior (territorial behavior) matures so early in Steatocranus casuarius that the animal has it available as soon as it is independent as adaptation to a particular habitat.

Steatocranus—like certain other strictly bottom-dwelling cichlids (Teleogramma, Lamprologus) and all species of the North-American etheostomatids (Winn, 1958)—no longer possesses an air-bladder. Like the bullhead (Cottus gobio), they all vigorously defend a territory already as minute juveniles—a territory they require for staying concealed. In these instances, we can hardly speak of reproductive motivation, and this even less in the case of the numerous coral fish species (chaetodontids, pomacanthids, and pomacentrids), which already as juveniles defend their foraging range during the entire year, where, in part, alone the "poster colors" are adequate for pre-warning. Some species (numerous pomacentrids, Pomacanthus arcuatus, among other ones) acquire plain coloration as sexually mature, paired animals, and become non-aggressive in order to defend their territory together.

We must entirely separate the questions regarding the functions of a territory, and regarding the phylogenetic derivation of the behavioral responses bringing about demarcation of a territory. In all these fishes, the territory, first of all, provides concealment and covers the food requirements; in this case, feeding and agressive behaviors are primarily active; the territory serves in reproduction only in a secondary manner.

Literature contains numerous references to cases of territoriality in fishes; the establishment of these territories appears to be based on fighting for food and not to be associated with reproductive behavior; association with the latter behavior has been established in no case.

In Aequidens portalegrensis, both males and females occupy territories outside of the period of breeding (Ohm, 1958), as is the case in Pyrrhulina vittata (Schapitz, 1962). In Ambloplites rupestris, Lepomis cyanellus and L. megalotis, Gerking (1953) established site tenacity in the natural habitat for up to four years. Greenberg (1947) observed Lepomis cyanellus juveniles, which were as yet not stimulated by sexual hormones, to main territories. Numerous salmonids possess distinct foraging territories already as juveniles (Stringer, 1955; Hoar, 1958; Fabricius, 1955). Their aggressivity probably is elicited by very simple visual stimuli: Moving objects of appropriate size (Kalleberg, 1958), *viz.* food items.

In *Badis badis*, territorial behavior is seen for the first time with appearance of the first transverse stripe. The territory appears to be determined by the food supply (Barlow, 1963). Kalleberg has described numerous examples of fish territories, which served solely for foraging.

Apparently the same is valid in birds: Great spotted woodpeckers occupy foraging territories outside of the breeding season; that occupation promotes the formation of breeding territories. Even in so-called solitary breeders—like great tits, for instance—the alpha-animals of the winter swarm had their territories nearest the feeding site (Kalela, 1954)

The territory, thus, may be first of all a foraging territory; we are not justified to assume in a general manner that reproductive drives represent the motivation for territoriality. Although Wickler has suggested that in the case 282
of *Steatocranus*, this assumption is wrong, with certainty, in the case of *Haplochromis* (Kirchshofer, 1953). In the latter case, the breeding territory has evolved from the foraging territory.

There exist exceptions: In the few passerines, which remain together on their territory during the entire year in close pair cohesion, it is probable that territorial behavior has evolved from reproductive behavior; this would be the case, for instance, in the common raven, although the territory may also in these birds serve above all for foraging (Gwinner, 1964).

There then exist also territories established due to reproductive motivation. The questions after phylogenetic origin, behavioral motivation and ecological function must be raised anew in each instance.

2. Territorial behavior of the Haplochromis female

(a) Present knowledge - According to Baerends (1950) the mouth-breeding females occupy a special position among the cichlids, since they do not possess territories; the latter author, nevertheless, stated that these females defend the pit of the male, and this even against the male. According to Kirchshofer (1953), Haplochromis desfontainesii females become territorial only for brief periods of time, when they defend a source of food. According to Wickler (1962), typical mouth-breeding females are more congenial than substrate-breeding ones, since they do not have to defend a territory; they never lead their young into the "no-man's land" of the upper water layers. In the case of Hemihaplochromis multicolor, the female is present on a male territory already one to two days prior to spawning; she digs there, chases other females away, fans over an imaginary clutch of eggs—i.e. she exhibits, in the form of a non-functional rudiment, the same sequence of motor patterns used by substrate-breeders, like Hemichromis, for instance, to fan oxygen-rich water toward the spawn—and stays also after spawning for a day or two on the male territory. This female then possesses a small breeding territory.

Territorial behavior may also be seen in the females of the typical mouth-breeders, like H. wingatii and H. burtoni.

(b) Territorial behavior (apart from fighting) - Females bearing eggs lose their longitudinal stripe shortly before releasing the young, and move about less, just like the males when they start to become territorial. Gradually there appear transverse stripes on the body. In the case of the head pattern, only the eye stripe is present at first; the other stripes are only indicated and, under certain conditions, become fully evident only after the young have become independent. The females move down to the bottom and defend a certain territory against other females. If the aquarium is already divided up by other females, the newly introduced female acquires transverse stripes and attacks only if the other females fight each other. That, however, occurs only rarely, since supernumerary animals usually are used as "whipping boys;" this "bicyclist response" (cf. page 278) can be elicited by guarded shooing of a female with young swimming about in the aquarium: She will attack a "whipping boy;" however, if that is a female about to release her young, and if the leading female is shooed to forcefully, the latter will flee and will then be attacked by the "whipping boy." A female in that state even attacked fighting males.

Once the females have obtained a site by fighting—which, in contrast to the male colonies, must be shaded—they usually permit the young to swarm out at the bottom. There, the females immediately start to feed after their prolonged fast. (They almost never take up food while carrying.) While doing that, the females also do some digging, but not at certain sites, as is done by the males, 28 but in an undirected manner. I have observed only one such female to clean a bottom site, measuring about 4.5 cm in diameter, of dead leaves, and to deepen it somewhat. This digging—as reflected by the behavior—like that of the males reflects aggressive motivation. The beginnings of aggressive feeding can be seen when a leading female feeds hastily not at any site, but along the boundary of the territory.

(c) While leading young - The readiness or motivation to pick up young is in evidence up to six days prior to swarming out (cf. also Reinboth, 1956). One day before release, the female actually picks up young, and when she finally releases them, she prevents their immediate return into her mouth by swimming rapidly backward. Frequently, the female swims immediately toward the bottom, i.e. she moves below the swarm. In that manner or by swimming past the swarm, the female disperses the swarm also at other times, when the young swarm around her mouth. I have observed only very rarely actually collecting of the young, as it is known in the case of other cichlids, and then only after the first release. In cases of danger, the female, with head tilted down, swims back over a short distance and snaps up the young closets to her; the other ones follow immediately. "Yawning" (gaping) exerts no effect on the young.

This swimming below or around the swarm, just like the swmming backward prior to taking the young back into the mouth, is an avoidance movement, because it is possible to induce backward swimming and, thus, picking up of the swarming young by guardedly disturbing the mother. The tendency of the female to give way increases with increasing timidity, and actually timid mothers pick up their young much more frequently and for longer periods of time than do aggressive ones—and this, witnin certain limits, independent of the number of young. The young swarms of timid females also stay much more closely together than those of more aggressive females, since the former stay more at the center of their territory—a fact, which, no doubt, enhances the site tenacity of the young in conjunction with the frequent pick-ups (Albrecht, 1963).

Occasionally it looks as if the female were actually fleeing from the young, and she will swim up and down along the aquarium plate, something an aggressive fish exhibiting transverse striping never does at other times. If an alarming incident occurs, the female stops briefly and the young swarm quickly back to the mother's mouth.

Intrusive young induce aggressive females more rapidly to give up their readiness to pick up young than timid females. If a vigorous attack of a female in response to some alarming stimulus decreases, the female's escape drive increases and, thus, not only her motivation to pick up the young, but also the motivation of the young to swim back to the mother's mouth: An aggressive female vigorously chased a fish through her territory; thereupon the young swarmed around her mouth without success, and a timid female on the next territory picked them up.

The time between pick-up and release of the young depends on the intensity of the eliciting stimulus. Toward the evening, the young are particularly ready to swarm back to the mother's mouth, and the female is particularly ready to flee and, thus, to pick up the young, so that recovery over night is doubly ensured.

In the aquarium, territoriality is not discontinued once the young become schoolers and have left the territory of their mother; frequently, territoriality increases even further. The motivation to give shelter, thus, does not simply disappear or is reduced solely by aversive stimulation, but is also suppressed by the rise of territoriality and, thus, the decline of escape motivation. According to Reinboth (1956), the *Hemihaplochromis multicolor* female defends her young still after conclusion of the period of leading. Also in this instance, aggressivity is not associated in the first instance with the young; 284 this is in contrast to leading geese, where the pair with the youngest gooselings usually has the highest rank (Heinroth, 1910).

On the basis of similarities in courting behavior, Wickler (1963) suggested that *Tropheus moori* is more closely related to *Haplochromis* than to *Tilapia*, in the proximity of which that species had been placed earlier. The observation of a leading female confirmed that suggestion: This particular female stayed in a certain crevice, from which she chased other fishes away. Between the individual attacks, she fed on the bottom, and this also as vacuum activity. The readiness to take in young increased after she had chased a fish away. When the surroudnings were entirely sedate, the young moved away beyond sight, up to 40 cm away and returned on their own. These behavioral patterns correspond to those seen in Haplochromis (Albrecht, 1963); hitherto, they are not known in the case of Tilapia species.

(d) Discussion - If Peters (1937), Kirchshofer (1953) and Reinboth (1956) call the facial pattern of leading females 'mother dress,' we must state that this is a "prejudicial" term (Hassenstein, 1951), which indicates a phenomenon, without describing it. We actually see a facial pattern resembling that of the male, when females in aggressive mood feed on a large titbit (cf. p. 277). Two females exhibited that pattern right after spawning: One, kept in an aquarium measuring 250 x 200 cm, acquired a distinctly male coloration, defended her territory (located away from the male colony) against both females and non-territorial males, and, after she had been chased away by a male, did not immediately acquire female coloration, but was initially colored like a non-territorial male. Another female, which I transferred a quarter of an hour after spawning into an aquarium previously known to her, acquired a "mother dress" of supernormal distinctness, which corresponded to the coloration of very young, just territorial males.

Within three to four days, these two females turned into "moving fish" with longitudinal stripes, normally appearing only after spawning. The females then moved away from the courting arenas of the males and established their territories at shaded sites providing protection, where the young could grow up undisturbed.

The territorial behavior of Haplochromis females, thus, exhibits two peaks: During spawning (p. 289) and when releasing the young.

Territorial motivation arises in the female not only in connection with the breeding cycle, but also when she defends her foraging site—this, however, in a less intense manner, and that motivation is more readily abandoned on being alarmed. This ready abandoning of territory outside of the breeding cycle is just as intelligible as the stubborn defense of the "young territory."

The territorial motivation of the female is reflected not only in the patterning, the fighting (cf. p. 287) and the digging; the pick-up of the young can also be traced back to the motor patterns of feeding and, thus, is related in its motivation to territorial behavior. The female moves both the eggs and the young around in her mouth like badly tasting food. In anthropomorphic terms: She does not want some other individual to eat her young, although she herself does not like their taste. In functional terms, this behavior would be food jealousy.

Motor patterns associated with feeding, thus, have a function not only in aggression as "raw material," but may also be subject to a change in function in the service of parental (maternal) care.

Leading (or guarding) of the young is caused by behavioral elements belonging to the complex of territorial behavior.

D. Fighting 285

1. Fighting between males

During interterritorial boundary fights—no doubt, the most frequent type of fighting in both H. wingatii and H. burtoni in their natural habitat—the opponents approach each other almost frontally with spread fins. Just before they meet, they either swim simultaneously back and then advance again, or alternately move back and forth together. This form of fighting, the pendulum movement (Albrecht, 1963, Film), has also been described by Lorenz (1953) in Etroplus maculatus, by Oehlert (1958) in Cichlasoma meeki, and by Wickler (1958) in Steatocranus casuarius.

During the forward rush, the conspicuously black ventral fins are spread and turned toward the fighting partner. The readiness of the pendulating individual to swim forward or to stop, respectively, can be read from the movements of the dorsal fin. During aggressive forward swimming, that fin is folded; during stopping or backward swimming, it is keel-like unfolded and prevents rolling movements. Fish species living in calm waters and moving about little, for that reason, frequently have a leaf-shaped body.

Using the pectoral fins, the pendulating fish swims backward; during the forward rush, the tail is spread and pushes the body forward; during the backward move, the tail is folded, and the pectoral fins do the work.

During pendulum movements, forward swimming and backward swimming are brought about by different fins, and we are dealing here with true threat behavior to the extent that the aggressive drive controls the driving, unpaired fins, and the escape drive controls the braking pectoral fins.

If a timid fish tries to conceal itself in a crevice, all fins are arrested apart from the pectoral fins, which beat lightly in the backward direction. [In completely sedate fish, movement of the pectoral fins is also arrested, probably because the recoil associated with the stream of respiratory water (Breder, 1924; 1926) is balanced by body friction.] If the fish is alarmed at that point, the pectoral fins first beat again backward, and the fish moves back. Next, the soft part of the dorsal fin begins to beat, and then also the upper part of the tail fin. Finally, the conflict between these two motor patterns becomes so pronounced that the forward move predominates, and the fish rushes about in the aquarium in an undirected manner. In the natural habitat, the fish would then be escaping. The tail fin-beats under these conditions are not activated by the fighting drive, since the fish is escaping and not attacking. The eye stripe—also a sign indicating aggressivity—can never be seen in that situation. The escape drive activates the pectoral fins as well as the tail fin, but the pectoral fins are activated first, as in the case of fighting.

When these fish meet at the common boundary, they open their mouths wide and approach each other until their mouths touch, exactly in the manner described by Baerends (1950) in *Tilapia mossambica* as "mouth smacking." If the fight continues, the opponents pass each other quickly, and each one tries to butt the partner's flank. However, since both are moving away, injuries are rare. The partners may circle each other rapidly several times in this manner.

Following this "circling," the two partners return to their respective territories and pendulate back and forth along the boundary, or they stop at the border and show the lateral display threat with spread pectoral and tail 286
fins beating in opposite directions; this aspect is particularly striking when the fish in that posture swims back a little distance (cf. the films: Lorenz, 1957, *Hemihaplochromis*, fighting between two males; Wickler, 1962, *H. burtoni*, courting and spawning; Albrecht, 1964, *H. burtoni*, fighting between two males); the ventral fins move up and down in a quivering manner, while turned toward the opponent; the latter, with dorsal fin rhythmically beating up and down (as during the pendulum movement), takes up a position at an acute angle with respect to the partner showing the lateral display threat (T position). After a while, the one standing at an angle suddenly turns toward his opponent, whereupon the latter shows his broadside. In this way, the T position can be changed several times. The partner standing at an angle does not bite his opponent's flank, but makes snapping movements into 'empty space,' and this occasionally directly onto the flank of the partner, without, however, doing injury (cf. p. 290, spawning).

A biting inhibition in similar situations has been observed by Seitz (1949) and by Oehlert (1958) in their cichlids. In the Pelmatochromis kribensis female, that posture has turned into a highly ritualized consummatory geste (Heiligenberg, 1964).

The films dealing with fighting in Tilapia mariae, H. burtoni, Tropheus duboisi (Albrecht, 1962; 1963; 1964) and Hemihaplochromis (Lorenz, 1957) show that the individual showing the lateral display threat is bitten only if he gives up his rigid posture. That posture probably is brought about by the fact that the two drives—escape and aggression—innervate antagonistic muscles (Wickler, 1957). Heiligenberg (1963) has investigated the combination of contrary movements and the relative intensity of motivations with respect to each other: "If one fish gets set to bite, it is possible to transform the impending bite into either a lateral display threat or tail-beating by executing an alarming signal (let us say, a rapid hand movement in front of the aquarium), as long as that signal is not too strong and elicites escape" (l.c., p. 361).

If, during the lateral display threat, one drive becomes stronger than the other one, the fish in question gives up its rigid posture and, thus, stimulates the partner to perform biting.

The escape-aggression conflict evidenced by the fin movements has led to the sideways tail-beat as a special fighting element. In Haplochromis as in numerous other cichlids, sideways tail-beating is seen frequently during the lateral display threat, with the fish not moving, since the pectoral fins compensate the forward thrust of the tail fin.

According to Oehlert (1958) all muscle segments of the one side of the fish's body contract simultaneously during the tail-beat and, thus, suppress any forward move. Sideways tail-beats of that type may be seen in Cichlasoma *biocellatum* and *Herichthys cyanoguttatus*. During fighting, these fishes beat with the tail and, furthermore, butt with the head. In some cases, it may occur that sideways head-beating and tail-beating start at the same time with equal intensity, with the longitudinal muscles of one side contracting in unison (Burchard, personal communication).

According to Wickler (1957), the pectoral fins are spread during sideways tail-beating in order to balance the fish. Barlow (1962) saw *Badis badis* use the pectoral fins as brakes during tail-beating. In the fighting films of *bimaculatus* (Lorenz, 1963) and *Hemihaplochromis* species (Lorenz, 1957), the tail actually beats like a whip. When performing such tail-beats, it, thus. would be impossible to stay at a site without the assistance of the pectoral fins.

According to Oehlert (1958), the intraterritorial fight of *Hemihalpchromis multicolor* originally was a fight aimed at doing injury. Fights may be induced 287
by placing individuals together into a small aquarium—individuals, whose fighting drive has been dammed up by separate maintenace. When placing two indivudual together into such an aquarium, we may see very frequently the entirely different behavioral pattern of the "intraterritorial fight," in which two males fight for the same teritory. In the natural habitat, analogous situations would arise only extremely rarely. As colonial breeders, *H. wingatii* and *H. burtoni* (Albrecht, Film, 1964) do not possess an injury-inducing fight pattern. Their ritualized interterritorial fighting may erupt at any time, as long as the colony exists. Injuries are obseved almost never.

In the case of *Hemihaplochromis multicolor* we may assume the occurrence of colony formation also in the natural habitat—at least, the ability to form colonies. In an aquarium measuring 120 x 80 cm, four to five males established their own territories and performed only ritualized interterritorial fights.

The opposite movements of the pectoral fins and the tail fin—primarily a conflict between swimming forward and swimming backward—are employed not only during fighting. Pomacentrids and gobiids dig a pit by moving the fins, and, in fish providing parental care, these movements have developed into egg fanning.

In fighting, thus, elements associated with feeding behavior and elements of locomotion are employed, with the escape drive and the aggression drive directing different locomotory organs.

2. Fighting between females

According to Peters (1941), "only the representatives of parental families (for instance, *Hemichromis*) have available the same drive disposition in both sexes; in the father families (for instance, sticklebacks) or in the mother families (for instance, *Haplochromis*), that disposition is sex-specifically different."

It has already been demonstrated that the *Haplochromis* females possess territories like their males; their interterritorial fighting also is identical in all details. Pendulum movement, mouth smacking [i.e. fighting each other by pushing with the mouths], butting, circling, and the lateral display threat do not differ, in qualitative terms, from the corresponding behavior patterns exhibited by the males, i.e. they can be homologized on the basis of the second criterion. The patterning, too, is almost identical, since the abdominal fins become dark along the anterior edge, as in males measuring about 2.5 cm in length. According to Kirchshofer (1953), fighting *Haplochromis desfonatinesii* females also start to resemble their males with regard to coloration.

According to Lorenz (1963), the difference in the drive disposition is based on the quantitative difference of qualitatively identical movements and, thus, the role they play in the behavior of the males and the females, respectively.

The different frequencies of movements performed by males and by females, respectively, probably are due to the differences in the threshold values, at which the respective motor patterns respond during rises of activity-specific excitation.

The quantitative differences in male motor motivations and female motor motivations have been adapted to each other in the evolution of the species in a manner ensuring that their roles are distributed appropriately over the two sexes. In their interplay in reproductive behavior, the difference in their drive dispositions is in evidence more prominently than the fundamental, qualitative uniformity of their motor patterns. For instance, if we place a female into a large aquarium occupied completely by male territories, we will see absolutely nothing of female territorial behavior patterns, since these patterns 288 are completely suppressed by the stronger males. Only if we place several females of equal size into one aquarium will we see that the females defend territories exactly like the males, which territories then frequently are not bigger than the male ones. It is not known whether leading (guarding) females form colonies in their natural habitat; however, on the basis of the behavioral patterns observed, we could readily imagine such formations to take place.

Males and females have available the same inventory of motor patterns also during spawning (cf. p. 289).

E. Courtship

If a female appears, territorial males of both H. wingatii and H. burtoni usually leave their pit and (1) swim toward the female with vigorous tail beats, with the body slightly tilted forward and head pointing down. Quivering, they (2) display their pectoral region to the female, and then (3) return to the pit with vigorous tail beats (Wickler, Film, 1962; 1963); frequently, the males immediately turn around and repeat this sequence. During the entire sequence, the pectoral fins are braking the forward movement of the male; as long as one does not realize that this braking is taking place, one is surprised to see that the fish does not move more rapidly through the water considering his vigorous tail beats.

Braking in a similar manner (these fish swim toward titbits, (2) frequently turn rapidly around with a single tail beat right before reaching the titbit, and (3) do not flee far, turn around, snap at the titbit, and flee again. In these instances, too, we can draw comclusions regarding the braking action of the pectoral fins during backward swimming only on the basis of the intensity of the tail beats.

The sequences of movements can be compared and, in accordance with the seconf criterion, can be homologized. The facial pattern is always distinct during courtship, and frequently distinct during feeding.

Seitz (1952) called this homologous sequence in Hemihaplochromis species "turnaround swimming" ("Umkehrschwimmen," "dancing")—a term retained in the present paper.

(Cf. page 292 for observations permitting application also of the third criterion.)

Females exhibit turnaround swimming in front of subordinate females:

Female B, which has not yet picked up young, approaches, in tense posture, Female A which has picked up her young and, thus, has given up her territory. (On the basis of the behavior exhibited by Female C, which attacked Female A immediately after the pick-up, something she had never done before, such a female—like A—must be regarded as being defenseless; this female had lost her facial pattern, and was concealing herself between plants.) The body of the threatening Female B was tilted slightly forward the head pointing down; the tail fin and the pectoral fins were beating in opposite directions; just before reaching Female A, she performed a vigorous tail beat, and then, still performing exxaggerated tail beats (and with braking pectoral fins), she returned to her territory.

When *Haplochromis* males have chased competing males, they usually break up their pursuit in a sudden manner with a tail beat, which corresponds to the turnaround swimming.

Lowe (1959) saw *Tilapia leucosticta* males bite females cruising about in schools, then immediately turn around with one tail beat, and lead to the nest. Seitz (1949) saw mistaken courting in *Tilapia mossambica* only in front of juvenile males. According to Seitz (1942), turnoaround swimming in front of females is ritualized in *Hemihaplochromis* species to such an extent that the male, also when he does not approach the female from the center of his territory, performs 28
a 180-degree turn. However, it is possible that the center of his territory is not defined right from the start—the male at first digs several pits—and his turnaround approach was started from a foraging site and, since such sites frequently are transformed into territories, he led back to that site.

Tropheur moori, a close relative of *Haplochromis* (cf. p. 284), clearly exhibited a fluid sequence of intermediate forms from relatively undifferentiated turnoaround swimming in front of objects to be attacked to courtship turnaround swimming:

A *Tropheus moori* male swims toward a conquered male, which is quietly hiding in a corner, performs a tail beat in front of the latter, and returns to his original site with weaving tail beats; following several repetitions of this sequence, the tail beat is intensified to quivering.

By way of intermediate stages, quivering, thus, can be homologized (third criterion) with the lateral display threat and tail beating following next in sequence.

Turnaround swimming during feeding, fighting, and courting is homologous, and is exhibited in the same manner in front of subordinate individuals and (large) titbits. In conflict with the escape drive, the feeding urge as well as aggression activate identical motor patterns.

F. Spawning

Females ready to spawn move about in the aquarium less than other fish without territory. Transverse stripes appear on the body, and these stripes reach down further than in the case of cryptic patterning; the abdominal fins frequently become black (co-shading). The facial pattern discussed on page 279 is distinctly evident; in correspondence, these females frequently attack other females. Following the turnaround approach of the male, the transverse stripes of the female frequently darken more deeply, and she follows the male (following response, Reinboth, 1956). It could be that this following response has aggressive motivation (p. 292), because the other behavior and the patterning of the female are similar to those of males about to establish territories as well as those of females about to release their young.

The turnaround swimming of all males close to the female at this point is intensified to a real dance; again and again, one of the males exhibits his broadside to the female, with the male usually standing at an acute angle with respect to the female, as in the T position during fighting. If the female turns away, the male chases her immediately. If she, however, swims toward the male, he occasionally moves the dorsal fin up and down—that movement, too, is exhibited during fighting between males—and starts to do some digging in the pit, which again is a sign indicating aggressivity. By this time, the male lies in the pit half on his side, with his broadside presented to the frontally standing female (T position). All unpaired fins are spread; the abdominal fins move up and down in a quivering manner, asymmetrically misaligned toward the female; the pectoral fins are exerting braking action. The view held by Wickler (1962), viz. that mainly the pectoral fins propel the male into that position, is not correct; that is done by the tail. The female points with her head towards the region of the male's anal fin (T position). After a few seconds, the male suddenly turns around and rushes the female, which thereupon presents her broadside to the male, as the male had done just a moment earlier; occasionally, the braking action of the pectoral fins is so strong, that the fish moves backward a short distance (Films: Lorenz, 1956; Wickler, 1962). Both showing of the lateral display threat and changing of the T position proceed in all details as during fighting (p. 286); this, however, a little less rapidly—in particular, in *H. burtoni*.

The female, presenting her broadside to the male, lays a few eggs, and 290 immediately turns toward the male, which, thereupon, glides over the bottom of the pit, in exactly the same manner as *Hemihaplochromis* males, which, in that position, fertilize the eggs. However, even before the *Haplochromis* male is able to fertilze them, the female has already picked up the eggs; next, the female snaps at the egg spot on the male's anal fin (Wickler, 1962) and at that moment receives, in her mouth, the sperm released by the male. The waving abdominal fins of the male showing the lateral display threat propel the sperm in that direction (the female's mouth). It would appear that the movements of the abdominal fins have undergone a change in function. During the lateral display threat, they serve in enlarging the body outline; in spawning, they serve for 'internal' fertilization.

Between the laying of the individual batches of eggs, the female digs. According to Peters (1937), the Hemihaplochromis multicolor female ready to spawn also digs. In the same species, Reinboth (1956) found also pebbles, in addition to eggs, in the mouth.

During digging as well as during picking up of eggs and during snapping at the egg spot on the male's tail fin, the gill covers are raised exactly as during threatening.

The pre-stage of snapping at the egg spot is exhibited by fighting fish during exhibition of the lateral display threat: The partner standing at an acute angle snaps into empty space close to the flank of his opponent. During spawning, the male snaps only weakly at the flank of the female, but the female snaps at the male's egg spot in a well directed manner. We may suggest that digging, picking up of eggs (derived from the latter activity) and the inhibited snapping at the flank of an opponent overlap in the female.

Following production of several batches of eggs (change of T position), the eye stripes of both partners go pale, and this, at first, only during broadsides standing, and then also during standing at an angle; the back becomes very light. Toward the end of spawning, the eye stripe reappears again first in the male, and his "picking up of eggs" may turn into biting: Guardedly he holds on to the female's tail. The female finally assumes a longitudinal stripe and swims away from the pit. She then visits other males, where the entire sequence is repeated.

Pair formation, the rudiments of which Wickler (1963) was still able to discern in Hemihaplochromis, is no longer in evidence in Haplochromis, since the females in rapid turns spawn at the pits of several males (Figure 3), and leave the colony following spawning.

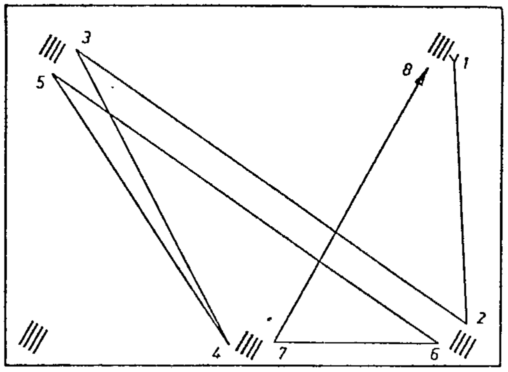

Figure 3 - Spawning by a female in the presence of several males. ////: Male holes. Duration 50 minutes. No. 7 spawning represented the final delivery of eggs by the female; at No. 8, the female exhibited only mock spawning.

Females just spent are more vigorously courted than females cruising in schools; that may be due to the fact that the spent females move about more sedately than the members of a school.

Table 2 surveys the corresponding (homologous) motor patterns observed in males and females, respectively. The horizontal columns show the homologous behavioral elements exhibited by males and females. The vertical columns show the similarities of behavioral and marking patterns associated with acquisition 291 of territory, and of the specific features of territorial and aggressive (fighting) behavior. The doubly framed columns served for homologization of spawning behavior and elements of fighting behavior.

For homologization of spawning and fighting behaviors, I have used almost exclusively the second criterion. Observations permitting use of the third criterion are described on page 292.

As suggested already on page 284, the territoriality of the females exhibits two peaks.

Table 2 - Homologous behavior patterns in the two sexes.

	Male	Female with young	Spawning female
Territorial behavior	Longitudinal stripe disappears	+	+
	Urge to move about decreases	+	+
	Lateral stripes extend further downward than under conditions of crypyic coloration	+	+
	Entire underside of body becomes dark	Only abdominal fins and lower lip are dark	+
	Dorsal fin becomes iridescent	anterior parts, occasionally	+
	Aggressivity increases	+	+
	Territorial in colonies	?	+
	Nesting hole with "threshing" floor	Digs, mostly undirected	Digs in the nest hole of the male
	Attachment to territory not absolute	+	+, on the contrary
	Colony at well illuminated sites	Territory shaded	-
Fighting behavior and spawning behavior	Pendular movement	+	+, but only with females
	Mouth smacking	+	?
	Circling, changing of the T position	+	+, earlier with females and during spawning; at that time, more slowly than during fighting
	Showing of the lateral display threat Pectoral and anal fins are beating in opposite directions Abdominal fins are moving—fluttering—toward the partner; the mouth snaps at empty space	+	+
	Biting is inhibited in the partner swimming at an angle, with the dorsal fin showing a quivering up and down movement		
	Trembling, ritualized showing of the lateral display threat, only in H. burtoni	+	+

Relationships between fighting and spawning

A. In *Haplochromis*

The motor patterns of the males and those of the females do not differ at all in qualitative terms, and the qualitative differences existing may be obliterated entirely in exceptional cases or under particular experimental conditions, so that homologization of fighting and spawning behaviors becomes possible also in accordance with the third criterion; that is important, since, according to Remane, the second criterion alone does not exclude analogies.

A female assumed a slate-grey coloration during spawning—a coloration 292 occasionally seen in elderly females exhibiting "male plumage." She followed the male in a distinctly aggressive manner not only during turnaround swimming, but also when that male, following pendulum movements performed with another female, retired to his pit and, there, probably appeared to be less intimidating. These fluid intermediate stages support the assumption voiced on page 289 *viz.* that the "following response" is motivated by aggression: The female attacks the male as he turns away; males attack females, when the latter turn away from the pit. Oehlert (1958) observed a *Haplochromis desfontainesii* female, which performed the turnaround swimming sequence in front of the male, as he was turning away from the pit after spawning. I have seen the same thing in *H. wingatii*. The females of these species then possess the potential to perform this highly differentiated sequence of motor patterns considered to be a male property, and employ it in front of the other sex.

In an aquarium occupied by only a few *H. wingatii* females, the two largest ones behaved almost like males: They had established territories with a pit; fought each other; and exhibited turnaround swimming in front of the small females. One small female, which initially had been very aggressive toward females of her own size, finally spawned in the presence of one of the two viragoes; the latter "fertilized" the eggs, i.e. did not lay eggs. With regard to velocity, the circling performed in the pit was between the aggressive circling and the circling during spawning involving males and females. Following spawning, these two females circled outside of the pit almost as rapidly as during fighting, and this at first close to the bottom and then also without substrate contact.

The circling associated with spawning evident in the films dealing with mock spawning in Haplochromis strigigena (Lorenz, 1950) and in Tropheus duboisi (Albrecht, 1964) is distinctly less rapid than the circling associated with fighting (cf. the corresponding films: Lorenz, 1957; Albrecht, 1964), and is repeatedly interrupted by sudden attacks. Tropheus spawns and fights without substrate contact; the other Haplochromis-related species known to me go to the bottom for both spawning and mock spawning.

In the fights between females—just as in the turnaround swimming of the viragoes—one could clearly see intermediate stages between tail beating and courtship-associated turnaround swimming of the males. In that case—as also in that of the above-described H. wingatii female, which exhibited turnaround swimming in front of a male—the "courted" partner, during the third phase of the turnaround swimming sequence, followed closely and received several tail beats in the face.

On page 288, I have described the turnaround swimming, and explained it on the basis of a conflict between escape and aggression. As mentioned already at that time, that interpretation is not adequate to explain the third phase viz. the returning into the pit; why should a fish with braking pectoral fins (= propelled by the escape drive into the opposite direction) and driving tail fin (= propelled by the aggressive drive) swim to the center of greatest security? That question can be explained on the basis of the behavior exhibited by the just-described "courting" females: The (aggressively) following partner is fought with tail beats until it has entered the pit. In order to be able to do that, the pectoral fins must brake. In courtship normally seen, this conflict movement probably has been ritualized and, thus, has become independent to such an extent that it is performed also when the partner does not follow immediately.

The biting inhibition, elicited by a fish exhibiting its broadside, could be clearly recognized when a virago, which used to chase all other fish away (in particular, if they were feeding or fighting at the bottom), only butted a certain fish not fleeing from her, with that butt being placed in the region of the anal fin.

The finding showing that fighting patterns are employed during spawning 293
in hardly modified form may be understood as follows: The genus Haplochromis with very great probability has evolved from forms closely related to the genus Hemichromis. All species of that genus form cohesive pairs, and spawn very peacefully following rather complex pair formation procedures. Pair formation has been lost in a secondary process in Haplochromis as also in certain other mouth-breeders, and the aggression-eliciting encounter conflict (which is eliminated in the pair-forming cichlids by pair formation) continues right up to the spawning event. In that way, motor patterns associated with fighting could turn into those associated with spawning; these patterns have only been "defused" by the biting inhibition described on page 286.

B. Convergent behavioral adaptations in other fishes

Fishes primarily not forming pairs—to be discussed in a moment—also employ fighting patterns during spawning; however, since most authors have not paid attention to this particular aspect, detailed homologization and discussion of fighting and spawning behaviors frequently is not possible.

Anabantidae - Spawning materializes on the basis of ritualized attack and escape motor patterns (Kuehme, 1961).

Blue perch or 'chameleon fish' (Badis badis, Nantidae) - The males and females circle each other during spawning as well as during fighting. The female exhibits distortion of her mouth—an element seen in fighting males only during extreme excitation. The female usually is territorial prior to spawning; the male is always territorial (Barlow, 1962).

Eupomotis gibbosus (pumpkinseed; sunfishes, Centrarchidae) - The fighting males circle each other with tail beating. During spawning, the males and the females circle each other, with the females exhibiting tail beating (Noble, 1934).

Characins (Characidae) - *Anoptichthys*, *Aphyocharax*, *Roeboidea*, *Metynnis*, *Hemigrammus*, *Pristella*, *Hyphessobrycon*, and *Copeina* fight by swimming side by side with tail beating. During spawning, the males and females swim side by side on the surface of the water and, then, suddenly separate with one tail beat while spawning takes place. The parallel swimming during fighting of *Noemacheilus kuiperi* resembles the spawning leap of *Copeina arnoldi* (Wickler, 1962). Fighting *Copeina arnoldi* also swim towards the surface of the water. While fighting, *Pyrrhulina vittata* swim side by side; the dorsal and anal fins are bent towards the opponent, with the anal fin being cup-like arched. The males and females fight prior to spawning. During spawning the males and females swim side by side, with the anal fin of the male embracing the female (Schapitz, 1962).

Northern pike (Esox lucius) - The males and females fight in an identical manner. During fighting, the partners, swimming side by side with spread fins, now and then exchange tail beats. Biting occurs rarely, and then only in the form of light butting. 216

During courtship, the partners touch each other lightly with their mouths at either the head or the flanks. During subsequent parallel swimming, all fins are spread, and the branchiostegal membrane is raised as during fighting. Next, there follows a tail beat and jerking of the male's head; the female hits lightly back with her tail—and spawning has taken place during that episode. Between the laying of individual batches of eggs, the males are very aggressive toward each other. Females not yet ready to spawn and females almost spent reject males with head jerking, which is similar to the head jerking seen during feeding: They jerk with the head towards the opponent and back to the median, and not further (Fabricius and Gustavson, 1958). The male exhibits the same movement during the spawning event (Fabricius, Color Film).

Salmonids - Fighting Salmo gairdneri circle each other during fighting and, in a similar manner, during spawning (Stringer and Hoar, 1955). Coregonus lavarctus have a peculiar lateral display threat, the "sailing;" during spawning, the two sexes swim to the surface in the sailing posture (Fabricius and Lindroth, 1954).

Thymallus thymallus swim side by side during fighting, spread their fins, 294
lower the branchiostegal membrane, and tremble at maximal fighting intensity. That trembling resembles the courting of Salmo alpinus, S. salar and S. trutta. Shortly before, and after, spawning, the females are highly aggressive and fight with the males. During spawning, the partners swim side by side, spread their fins, lower the branchiostegal membrane, and open the mouth. During the morning hours, these fishes are not territorial and do not spawn during that time (Fabricius and Gustavson, 1955).

Salmons (Salmo trutta, S. salar) - Fighting occurs during feeding, when these fishes are territorial, and during courtship. Foraging fights and courting fights frequently cannot be distinguished with regard to their appearance. Titbits, which the individuals are unable to master on first attempt, are shaken and repeatedly snapped up. If that titbit is too large, the fishes make the same movement into emplty space, as they do also when the "prey" is a member of their own species.

Prior to fighting, the partners display in parallel position, spread their fins, raise the gill covers, open the mouth, and tremble with the whole body; fighting frequently takes place with raising of the gill covers, parallel swimming, tail beating, circling, and biting. The females, during fighting, swim side by side over a large distance; they bite less.

Prior to spawning, the female digs a pit (redd) in the gravel, and this with the aid of tail beats, the locomotory coordination of which corresponds in every detail to the tail beating seen during fighting. The female spreads the fins and raises the gill covers, opens her mouth, and becomes aggressive toward other fish; in between, she performs feeding movements into empty space. During digging with open mouth, she directs her tail beats towards the male; in between, there occurs some serious brawling. During that encounter, the partners swim side by side with open mouth and spread fins, and circle each other. During spawning, only the element of circling is missing (cf. Film, Fabricius, 1954). During spawning-associated trembling, we may see the same behavioral patterns as during digging (Jones and Ball, 1954).

The afore-mentioned authors differentiate between fight-associated trembling (quivering), courtship-associated trembling, digging, and spawning-associated trembling. They traced fighting-associated trembling back to spawning-associated trembling. Fabricius and Gustavson (1953; 1954) also believed that courting represents a spawning event of low intensity.

I believe we are not permitted to regard all behavioral patterns just described as phylogenetic derivatives of the spawning act; the reasons are the same as in the derivation of territorial behavior from courting (sexual) behavior (cf. pp. 281 - 282).

Fabricius found it surprising that courting and fighting can be mixed. However, once we remember that courting is only a derivative of fighting, the relationship becomes evident.

Numerous salmonids assume a light back during both fighting and spawning (cf. Albrecht, 1962, Co-shading).

Observations in the stickleback

According to my own observations, the three-spined stickleback (Gasterosteus aculatus L.) courts using motor patterns, which, in part, can be traced back to motor patterns associated with fighting (cf. the films produced by Albrecht, 1963; 1964).

I. Feeding - Threatening

(1) When a stickleback happens to find a titbit, the fish points its head down, raises its spines—more steeply with increasing size of the titbit—and snaps at the food. This feeding posture is a signal for the other members of the swarm: The swarm dissolves, the members rush towards the titbit, also erect their spines, and try to rob the titbit.

(2) If one stickleback threatens another one by pointing its head down and erecting its spines, the threatened opponent either flees or resists and then returns the display. The two partners then are standing side by side with their heads pointing down, and, during more intensive threatening, they perform feeding movements at the bottom. In his first stickleback experiments, Tinbergen

regarded these movements as displacement feeding, and subsequently as nest digging as displaced activity (redirected activity). To the extent that one is permitted to draw conclusions regarding the stickleback on the basis of my _Haplochromis_ observations, the question, "Displacement feeding or displacement digging?" represents a spurious problem, and the behavior mentioned should be explained in accordance with the outline presented on page 278. It can also happen that feeding turns into pure threatening.

It would then appear that there exists a relationship between feeding and fighting in the stickleback similar to the one found in _Haplochromis_ and other forms.

Although the spines of the stickleback--as already mentioned further above—have a function in defense, they are erected also in conflicts between aggressivity and escape motivation.

II. The following behavioral patterns are exhibited at the nest: 295

(1) Fanning - While foraging, the fanning pectoral fins frequently send sand whirling upward in the water; the backward pressure of the pectoral fins counteracts the forward pressure of the tail fin, and the water current directed forward by the pectoral fins loosens the sand, thus, uncovering titbits. Fanning at the nest—which has a function in the supply of osygen-rich water required by the eggs as development proceeds, but occurs already prior to spawning—has the same locomotory coordination as fanning for titbits. In both cases, the fish bore their snouts into the substrate, and this frequently with erected spines; either they have found something edible, or they are building a nest. Nest-building, thus, must be derived from motor patterns associated with food seeking.

(2) The zigzag dance of the male can be divided into one aggressive component and one escape component (Van Iersel, 1953). Females ready to spawn respond with "presentation of the abdomen," erection of spines, turning towards the male, and biting (if the male comes too close) to the aggressive component "zig" (females not yet ready to spawn flee). (An attacked stickleback also exhibits the ventral side and raises the spines; in the female ready to spawn, that movement is ritualized.) Additional biting incidents may occur before they arrive at the nest.

(3) "Showing the nest entrance" - When performing this behavioral element, the male, head pointing down, stands at the nest entrance; his spines are erected; and now and then the male thrusts his snout into the bottom (cf. I. 2., Threatening). The female—which, also with head pointing down and erected spines, stands next to the male—responds to the brilliant eye of the male as she does to threatening (model experiments, Tinbergen, 1937); occasionally, there occur biting incidents, if the female is not yet fully ready to swim through the nest.

Females ready to spawn may "misunderstand" really threatening of males. Four males, which had just been feeding, were threatening each other within a confined space; suddenly, several females approached and "followed to the nest entrance."

(4) "Pasting" - The behavioral complex of "pasting," wriggling through the cluster of nest material, spawning, and fertilization of the eggs cannot be traced back to motor patterns associated with fighting.

During pasting, the nest-building stickleback male secretes a sticky glue from the kidneys, which pastes the nesting material together into a loose cluster.

By wriggling through the cluster of nest material, the male creates a tunnel, which is used by the female for spawning and by the male for fertilizaing the eggs.

All four behavioral patterns can be homologized since:

(a) The movements are almost identical in all cases, and the minor differences are bridged by intermediate stages.

(b) Frequently sperm is released already during wriggling through the nest material cluster (Bol, 1959), and also

(c) during pasting: In one case, in which a male was pasting his nest, containing a batch of unfertilized eggs, only on the outside, the eggs subsequently turned out to have been fertilized.

(d) Following passage through the nest, spawning, and fertilization of eggs, the backs of the males and females assume dark coloration; following pasting, that is frequently the case.

The ancestral motor patterns, no doubt, are those of spawning and fertilization; pasting can be traced back to the latter.

(5) Coloration - Females ready to spawn can be recognized by their light backs; frequently, the back has assumed even a bluish gloss, like the light back of the males in their attractive nuptial dress. The flanks of the two sexes are darker prior to spawning than normally. The different colorations of the undersides have turned into important releasers (Tinbergen, 1937), which prevent pair formation with the same sex.

Discussion of the results

A. Derivation of motor patterns of fighting from those of feeding

The following arguments indicate that motor patterns of locomotion and those of feeding have been transformed into motor patterns of fighting:

(1) Toothed jaws, including the motor patterns of their function, probably are phylogenetically older than intraspecific aggression;

(2) Fishes with different manners of feeding possess different manners of fighting;

(3) Feeding and fighting are positively correlated with regard to their appearances in time;

(4) The conflict between the forward tendency motivated by the feeding 296 drive and the backward intention motivated by the escape drive creates postures, which in every detail resemble those threat movements, which by definition materialize in a conflict between motor patterns motivated by aggressive urges and those motivated by the urge to flee (for instance, Daanje, 1950);

(5) The manner in which motor patterns of fighting can be traced back to those of feeding has been demonstrated in detail in the present paper in the case of Haplochromis.

B. Territorial behavior

The following arguments indicate that, in the cases investigated in the present paper, the roots of territorial behavior may be found in the complex of feeding and fighting, and not in reproductive (sexual) behavior:

(1) As the experimental results described on page 276 demonstrate, Haplochromis is more aggressive when feeding at the bottom than when feeding in the open water.

Territories are always located at the bottom; owners of territories are always aggressive.

(2) Ontogenetically, territorial behavior appears for the first time always following feeding, mouthing of sand, or during digging. The intensity of aggressive motivation determines the quantities of feeding, mouthing, and digging performed (cf. Heiligenberg, 1964). Feeding, mouthing and digging represent a fluid series of activities. Territories almost always have a pit.

(3) In no single piscine species has it hitherto been demonstrated that juveniles, with certainty, exhibit territorial behavior as pubertal phenomenon;

on the other hand, there are numerous species, which, as either juveniles or adults, possess foraging territories outside of the breeding season.

According to Tinbergen's definition, territorial behavior is dependent on reproductive behavior, and, actually, territoriality is found most prominently within the functional system of behavioral patterns associated with reproduction. However, since homologous territorial behavior can be found also in other connections, we must assume that that behavior has turned out to be so favorable for the synchronization of sexual partners, that it is most conspicuous in certain forms in that function. That, however, does not permit us to regard it as being ancestral.

Defense of reproductive territories, thus, represents only one—even if an important—case of territorial behavior.

C. Derivation of motor patterns of spawning from those of fighting

1. Courtship

Development of turnaround swimming in Haplochromis species—homologous in character during feeding, fighting, and courting—can be explained on the basis of a conflict between escape and aggression. In several species, that element has become independent due to ritualization.

2. Spawning

Motor patterns of spawning and those of fighting can, with certainty, be homologized in Haplochromis and, with great probability, also in other fishes. Even if homologization would have been possible only in accordance with the second criterion (which does not protect against confusion with analogous adaptive similarities), it would have been highly improbable that the homology of motor patterns established in that manner on the basis of a comparison of an 297 intraspecific system of functions was attributable only to analogy, since we cannot imagine any selective pressure that would have brought about an uniformity of motor patterns in two such highly different goals of adaptation, like, first, the distribution of the individuals over the habitat, brought about by aggression, and, secondly, the union of the sexes for the purpose of reproduction.

However, it has also been possible to apply the third criterion (transitory forms) (cf. p. 292).

The following arguments indicate that the motor patterns of spawning are derived from those of fighting, and not the other way around:

(1) Intraspecific aggression is more widely distributed in the animal kingdom than both courtship and pair formation; the latter is found only in animals performing the former.

(2) Ontogenetically, fighting occurs always earlier than spawning.

(3) At the onset of pair formation in fish, the conflict associated with meeting the partner always is reflected in agonistic movements.

(4) In fishes without pair formation, spawning represents the peak of the encounter (meeting) conflict, and this not only in species like Haplochromis, which have lost pair formation in a secondary process, but also in species, which primarily do not form pairs.

(5) Only the motor patterns "favorable" for spawning (because they are associated with biting inhibition), like circling and T position, have been taken over by sexual motivation. It is possible that the biting inhibition, which a broadside-standing fish elicites in one standing at an acute angle, represents an ancestral inheritance from predacious fishes: Prey fish, which cannot be snapped up frontally by the predator, are able to prevent being swallowed by either wriggling or spreading of the fins.

The following behavioral patterns cannot be explained solely by fighting motivation, but are motivated by the sexual drive, since involvement of the escape drive can be excluded:

(1) The circling associated with spawning appears more ritualized than that associated with fighting. That ritualization can be traced back neither to motor patterns of fighting nor to those of escape; it reminds one of the spawning movements of "normal cichlids."

(2) The eye stripe and a dark gill cover spot disappear following the laying of several batches of eggs—something that never happens during fighting following repeated changes of the T position. In fact, these patterns of markings or designs disappear also during escape motivation, which, however, can be excluded, since the fish not only continue spawning, but also do not exhibit any lowering of the threshold values for escape-eliciting stimulus situations; the opposite rather is the case: Once they have commenced spawning, the fish do not respond to even strong stimuli (for instance, [flash-light] photographing). It is certain that the transient reduction of aggressivity during spawning (described on page 290) represents an additional safety factor preventing that a fish already standing at the site is bitten.

(3) In the female, we find distinct snapping movements, in addition to picking at the egg spot on the male's anal fin—movements that are only indicated in the male. In fact, fighting males also snap at the flanks of their opponents, but extend both the maxillary and the intermaxillary and raise the gill covers as during frontal threat displays; the snapping of the spawning female, on the other hand, is something entirely different to the extent that it, in formal terms, resembles the digging and picking up of eggs. The snapping 298
movements seen during fighting, thus, can be traced back directly to the seizing of the prey; in the spawning female, indirectly by way of digging (cf. Films: Wickler, 1962; 1963).

D. Homology - Homonomy

The method of homologization has been established on the basis of comparative anatomy and phylogeny in morphological structures; since Whitman (1838), Heinroth (1919), Lorenz (1935) and, more recently, Hennig (1950) and Weber (1954), that method is applied also to behavioral patterns, i.e. patterns in time (Wickler, 1961). The study of functional changes is the most important source of knowledge in the area of ethological phylogeny.

Homologization is based on the comparison of structures of different organisms, and forms the basis for all natural systems. Inclusion of structures of behavior into this analytical approach may contribute to a significant extent to the sophistication of the system.

However, uniformly constructed parts in one and the same organism may also identified on the basis of the same criteria and established to be homologous (Remane, 1952). Homologous structures of that type, for instance, are the mouthparts and extremities of crayfish or the "normal body-shaking," the "demonstrative body-shaking" and the "double grunt-whistle" in the courtship of the mandarin drake (Aix galericulata) (Lorenz, 1941; Von de Wall, 1963). Such structures, however, are products of the same genetic material, i.e. they represent no direct source of knowledge in the phyletic investigation of organisms, except within the framework of the third criterion, for which reason they are called by Bronn (1858) not homologous, but homonomous.

In the studies dealing extensively with homologization of behavioral patterns —like those undertaken by Lorenz (1941) and by Faber (1952)—different species are subjected to comparisons; they serve in the sophistication of the natural system and, thus, are important for the phyletic consideration of organisms.

If we, as has been done in the present work, homonomize or homologize either in one individual or in one animal species behavioral patterns belonging to different functional systems, it should be possible to erect a natural system of behavioral patterns (with the aid of of the differentiation rule, Remane, 1952[1]). An attempt in that direction will be made in subsequent studies.

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[1] That rule states that, within a functional unit, originally uniform parts will become nonuniform with onset of division of labor. Functional units are (a) cells within an association of cells; (b) meristic organs; (c) bilateral or radial organs; (d) individuals of an association of species; and (e) different generations in alternation of generations.

The differentiation rule hitherto has been applied only to morphological structures. Would it not be possible to treat the functional systems in behavior like meristic organs?

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Translation of non-English bibliographical items

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58. Courtship and spawning in .....

59. .....: Courtship and spawning.

60. .....: Fighting behavior of the forcepsfish.

61. Fighting behavior of ..... (in the press).

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