Selective Feeding in Fish: Effect of Feeding and Defensive Motivations Evoked by Natural Odors

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Abstract—The effect of feeding and defensive motivations evoked by natural olfactory signals (food odor, alarm pheromone) on the choice and consumption of food items of different colors and tastes were examined in fish (koi *Cyprinus carpio*, roach *Rutilus rutilus*). Agar-agar pellets of red and green color containing one of the amino acids (glycine, L-proline, L-alanine; in the concentration of 0.1 M) were simultaneously given to single fish in pure water or in water extract of Chironomidae larvae or in water extract of fish skin. It was found that odors have different effects on the food-searching activity and food selectivity in fish. On the background of food odor, fish grasp pellets more often than in pure water. The equal choice of red and green pellets in pure water changes to a preference for red ones in the presence of food odor. Despite an increase in the absolute number of grasped pellets, their relative consumption is reduced and is replaced by a selective consumption of pellets with glycine regardless of their color. The increasing demand for food quality due to increased feeding motivation in response to food odor is an important adaptation enhancing the mechanisms of food selection and consumption. The defensive motivation caused by the alarm pheromone suppresses the feeding activity of fish. Fish grasp pellets several times less often than in pure water and reject most of them. There are no changes in color or taste preferences. The feeding behavior of both species is characterized by manipulation activity; it is higher in the cases of fish stimulation by food odor and when the pellet was finally rejected.

INTRODUCTION

Feeding behavior is a complex chain of events from the moment the animals receive the signal about the presence of food to its detection, assessment of its palatability, and consumption or rejection. It is evoked by stimuli of different modalities in specimens experiencing food motivation under starvation or insufficient satiation (Pavlov and Kasumyan, 1998). In many animals, feeding as a form of life activity occupies most of the diurnal time budget and is realized under different changing conditions against the background of natural fluctuations of light, temperature, and other parameters of the environment, under changing habitats and availability of food items, different stress loads caused by predation risk, and the appearance of competitors and parasites. These diverse exogenous and endogenous factors have a combined effect on the feeding motivation of animals while enhancing or increasing the effect of each of them (Colgan, 1993).

Trophic relationships are closely related to the defensive behavior. Feeding often occurs under conditions when consumers having access to food are subject to potential danger of attacks by predators. So, animals have to solve two important tasks—take a food and escape from predators. The defensive-feeding complex of behavior (triotroph system) is regulated by the ratio of feeding and defensive motivations and is considered to be an important and universal adaptation system (Manteifel', 1987).

Different aspects of the feeding behavior of vertebrate animals are actively studied by the example of fish, which are not only easy-to-use model objects but are diverse in the patterns and modes of feeding, food stereotypes, and life strategies (Pavlov and Kasumyan, 2002). Defensive and feeding motivations strongly influence fish feeding. Alertness and fear evoked by the risk of appearance or real presence of predators cause serious feeding disorders, suppressing its intensity, duration and effectiveness (Milinski, 1985; Gotceitas and Godin, 1991; Godin and Crossman, 1994). Increased hunger, as well as the presence of foraging specimens nearby and the feeding signals they generate, increase the feeding agitation of fish and stimulate food consumption (Beukema, 1968; Morgan, 1988; Young et al., 1990; Croy and Hughes, 1991; Pavlov and Kasumyan, 2000; Stoner, 2003; Stoner and Sturm, 2004; Martins et al., 2006; Priyadarshana et al., 2006). Fish satiation causes reduced feeding intensity and increased food selectivity (Ivlev, 1955). The effect of factors changing the motivational state of fish is estimated, mainly, with respect to their influence on quantitative characteristics of feeding. Changes in the qualitative composition of consumed food and the fish's ability to select food items have been studied less

thoroughly and, mainly, on the example of prey of one type that are different in size (Wootton, 1998; Mikheev, 2006).

Defensive and feeding behaviors have a polysensory basis. Olfaction plays a notable role in regulating these functions. The olfactory system differs from other sensory systems by distance perception, which provides earlier reception of the signal from remote sources (Atema, 1980). While stimulating the behavioral response, many odors have a primary effect and change the motivational state and physiological functions (Rehnberg and Schreck, 1987; Rehnberg et al., 1987; Lebedeva et al., 2000; Olsén et al., 2000; Moore et al., 2002; Stacey and Sorensen, 2006). The extent to which motivations evoked by odor signals affect taste preferences and feeding behavior and the ability of fish to choose and selectively consume food has been studied insufficiently. It is known that stimulation by food odor and by starvation causes shifts in taste preferences and modifies the testing of grasped food items (Beukema, 1968; Thacker et al., 1997; Kasumyan et al., 2009; Kasumyan and Sidorov, 2010a). The information on the effect of chemical signals of danger on fish feeding is contradictory. It is shown that kairomones and alarm pheromones change the intensity and selectivity of fish feeding only in the simultaneous presence of the visual image of the predator (Micheev et al., 2002). According to the data of other researchers, the isolated use of the alarm pheromone or its artificial analogs sharply decrease the amount of food consumed by fish (Smith, 1979; Mathis and Smith, 1993; Jachner, 1995; Irving and Magurran, 1997; Jachner and Janecki, 1999; Brown et al., 2001); strong fear, escape, and hide responses to the alarm pheromone suppress their feeding (Frisch, 1941; Marusov, 1976; Malyukina et al., 1977; Jachner, 1996).

The aim of this study is to assess the effect of feeding and defensive motivations caused by natural olfactory signals (food odor, alarm pheromone) on the selection and consumption by fish of food items differed in taste and odor.

MATERIALS AND METHODS

Experiments were performed on koi, a Japanese colored variety of carp *Cyprinus carpio* (six specimens, total length (*TL*) of 9–11 cm, weight of 17–23 g, two years old) and roach *Rutilus rutilus* (six specimens, *TL* 11–14 cm, weight of 11–20 g, three years old). The koi were purchased in the pet shop, and the roach were caught in the Vorya River (Moscow oblast). The fish were transported to the laboratory and kept separately in aquaria (80–100 L) with an inner filter for several months.

Two to three weeks prior to the beginning of the experiment, the fish were placed singly in aquariums with a slow water flow of 7.2 L in volume (30.5 × 20.5 × 15.0 cm, with a water level of 11.5 cm) with closed-loop water circulation. The water from the aquarium flow to the biofilter under the action of the airlift. The vision of neighboring fish was deprived by nontransparent side walls of the aquariums. There was no substratum on the bottom of the aquariums. Water from the biofilter flow (0.075 L/min) to each aquarium via a silicone tube (an inner diameter of 4 mm) directed downwards and fixed at a height of 5 cm above the bottom in the front part of the aquarium. The water flow along the long axis of the aquarium and was again directed by the airlift to the biofilter. A complete water cycle in the aquarium lasted 1.5 h. Pure water and solutions with food odor were introduced to the aquariums from the tank through a tube connected with the biofilter. The duration of delivery was 3 min at a rate 0.025 L/min. When pure water (control) and food odor solutions were delivered, the water flow from the biofilter did not stop and was at a constant rate (0.075 L/min).

Every day, a part of water in the aquariums was replaced by fresh water; the aquariums, tubes, and biofilters were periodically cleaned, and the activated charcoal was renewed. The water temperature was 20–24°C. The fish were fed daily with live chironomid larvae after the end of experiments. They were fed on the basis of the amount of food they could consume 15–20 min after its delivery to the aquarium. The uneaten food were removed.

In the first series of experiments performed on both species, green and red agar-agar pellets containing an water extract of chironomid larvae (175 g (wet weight)/L) were used. One pellet in the experiments with roach or two pellets of the same color in the experiments with koi were introduced into each of six aquariums against the background of pure water flowing from the biofilter. Pellets of different color were delivered at random. In the course of the experiment, which continued for no more than 1 min, the number of grasps of one introduced pellet (roach) and two pellets (koi) and the consumption were registered visually. The uneaten pellets were removed immediately after the end of the experiment.

In the second series of experiments with the same specimens of roach and koi, pellets were introduced into the aquariums 15 s after the delivery of pure water (control) or one of the food odor solutions, an water extract of chironomid larvae (roach or koi) or the skin of the tested species (koi). In each experiment, three red and three green pellets (roach) and two red and two green pellets (koi), each of which differed in the amino acid content, were simultaneously introduced into the aquariums (Fig. 1). Such alternative amino acids were L-proline and L-alanine in experiments with roach and L-proline and glycine in experiments with koi. The amino acid concentration in the pellets was 0.1 M. Amino acids were chosen due to their attractive taste for the examined fish species (Kasumyan and Morsi, 1996; Kasumyan and Nikolaeva, 2002). During each experiment, which lasted no more than 1 min, the
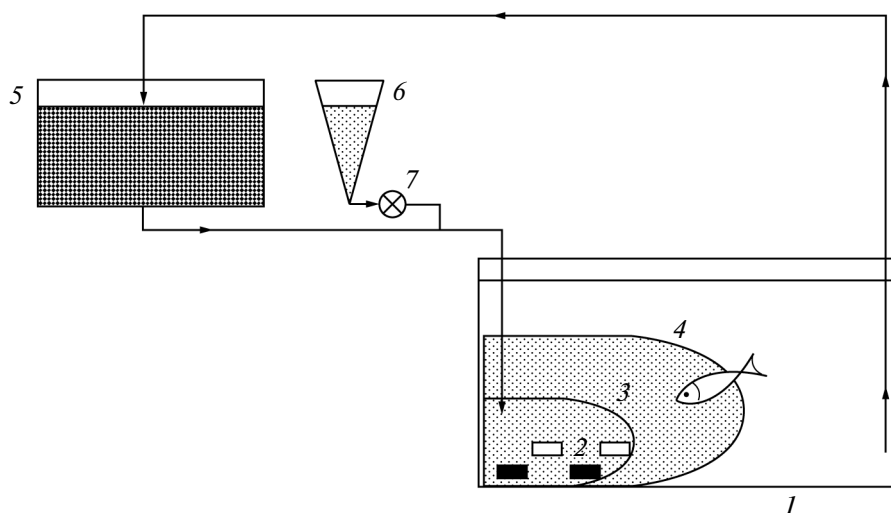
Fig. 1. Scheme of the experimental device with a closed loop water circulation: *1*, aquarium with a solitary fish; *2*, pellets of different type introduced simultaneously to the aquarium; *3* and *4*, the zone of odor spreading at the beginning and the end of extracts delivery (3 min); *5*, biofilter; *6*, tank with extract; *7*, valve.

number of grasps by fish of different pellets were registered visually. The uneaten pellets were counted and removed immediately after the end of the experiment. Experiments in pure water (control) and against the background of water extract of chironomid larvae were performed twice a day with an interval between sessions no less than 3 h. In each following session, red and green pellets contained an alternative amino acid. One to three experiments (often two) were conducted sequentially during the session for 3 min of flow of pure water or extract to each specimen. After the end of the experiments with water extracts of chironomids, two sessions of experiments were performed on koi against the background of the water extract of skin with an interval of 7 days.

Pellets were prepared from agar-agar gel (2%). For the experiments, agar-agar powder was added to hot distilled water; amino acid or the extract of chironomid larvae were added to the gel, together with either Ponceau 4R (5 µM) or Cr_2O_3 (0.3%) dye giving red and green colors, respectively. After mixing, the solution was poured into the Petri dish to form a gel plate. Cylindrical pellets were cut out of the gel with stainless steel tube just before the experiment. Pellets with amino acids were 3.5 mm long, and pellets with water extract of chironomid larvae were 7.0 mm long; the diameter of all pellets was 2.0 mm. The odor stimuli were solutions of water extract of chironomid larvae (10^{-2} and 10^{-3} g/L for roach and koi, respectively)[1] or the water extract of the fish skin of the tested species (10^{-3} g/L for koi). For preparation of water extracts, we used live chironomid larvae and the koi skin (fish length of 10 cm *TL*, weight of 20 g) cleaned

from muscles and scales and removed from the lateral surface of the fish body after a cold anesthesia (Mittal and Whitear, 1978; Zhuikov, 1989). Skin was stored at −18° C for no more than 7 days. After homogenization in porcelain mortar, the homogenate was diluted with water (1 g of biomaterial per 1 L of water) and infused for 15 min and then filtered through filter paper. The extract was diluted to the required concentration with purified water from the biofilter. All stimulus solutions were used in not more than 3 h after preparation.

The number of experiments on roach and koi with pellets containing water extract of chironomid larvae was 227 and 104, respectively (series 1). The number of experiments with pellets containing amino acids against the background of food odor in the aquariums (series 2) were 36 on roach and 63 on koi, and 24 and 79 experiments, respectively, were performed against the background of the extract of chironomid larvae. Thirteen tests on koi were performed against the background of the water extract of skin. Statistical analysis of the results was conducted by χ^2 criterion and the Mann−Whitney U test.

RESULTS

Experiments in Pure Water with Pellets Containing Water Extract of Chironomid Larvae (Series 1)

In this series of experiments, one (roach) or two (koi) pellets with water extract of chironomid larvae of either red or green color were introduced into the aquariums with the fish. The roach grasped about 70% of red and green pellets. Koi caught about 90% of delivered pellets, and like the roach, did not show any visual preference for pellets of a particular color. After grasping the pellet, the roach usually rejected it and grasped again several times; the average number of

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[1] Here and below, the concentration of extracts is the raw weight of chironomid larvae or fish skin.

Table 1. Responses of roach *Rutilus rutilus* and koi *Cyprinus carpio* in pure water to agar-agar pellets of various colors containing chironomid larvae extract, 175 g/L

Fish, pellet color	Grasped pellets, % of introduced pellets	Consumed pellets, % of grasped pellets	Average number of pellet grasps			Number of experiments
			upon consumption	upon rejection	all pellets	
Roach:						
red	76.0	61.6	1.51 ± 0.14	$3.32 \pm 0.52**$	2.21 ± 0.24	96
green	68.5	64.0	1.32 ± 0.12	$2.39 \pm 0.31**$	1.71 ± 0.15	131
Koi:						
red	94.4	99.0	1.06 ± 0.04	2.00	1.07 ± 0.04	54
green	88.0	95.5	1.02 ± 0.02	$1.50 \pm 0.50*$	1.05 ± 0.03	50

* and ** are the differences between pellet grasping in experiments on consumption and rejection are significant at $p < 0.05$ and $p < 0.01$.

grasps of red and green pellets was 2.21 and 1.71, respectively. Such behavior was less typical for koi, but the number of grasps of pellets of different color was the same. Koi consumed pellets more willingly; the consumption of pellets by the roach was 1.5 times lower. The consumption of pellets of different color by roach and koi did not differ significantly ($p > 0.05$, for the both species) (Table 1).

In experiments in which pellets were rejected, the roach performed repeated grasps more often than in experiments in which pellets were consumed ($p < 0.01$ for red and green pellets) (Table 1). Koi also demonstrated such a pattern of behavior, but a significant difference was found only for green pellets ($p < 0.05$). Such a comparison was not made for red pellets, because only one red pellet was rejected. When both species finally rejected a pellet, they ceased grasping it, swam aside, and did not return until the end of the experiment.

Experiments in Pure Water and Against the Background of Food Odor and Alarm Pheromone with Pellets Containing Amino Acids (Series 2)

Roach. The response of the roach to the simultaneous introduction into the aquarium of six pellets (by three pellets of red and green color, each containing alanine and proline) was weak. The number of registered grasps of all pellets in each of two variants of delivery was two times as less than the total number of introduced pellets, not only in pure water but against the background of the extract of chironomid larvae, which did not cause the search response in fish. The consumption of pellets with amino acids exceeded 30% of the delivered ones only in one case; in the other seven cases it was several times lower (Table 2). There were significant differences between the consumption in pure water of simultaneously delivered green pellets with proline and red pellets with alanine ($p < 0.05$) (variant 2) and between the consumption in pure water of green and red pellets with alanine ($p < 0.05$) (variants 1 and 2, respectively). In all other cases of pair

comparisons of the consumption of pellets, either in pure water or against the background of water extract of chironomid larvae, significant differences were not found.

Koi. In experiments with koi, two pellets of red and two pellets of green green color were simultaneously introduced into the aquarium. The smaller number of delivered pellets compared to the experiment with the roach made it possible to register the fish response to each of a pellet.

In pure water the fish grasped most of introduced pellets and the number of grasped pellets and the number of grasps did not depend on their type in the both variants of the experiment. The consumption of pellets with glycine was higher than those with proline regardless of their color but the difference was significant only in variant 2, in which the consumption was 1.27 times higher ($p < 0.05$) (Table 3).

In experiments performed against the background of added extract of chironomid larvae, the search activity of fish caused by food odor was not manifested, because both the koi and roach started their response to pellets immediately after they were dropped into the aquarium. The fish grasped a similar number of pellets of each of four types; as compared to the control (pure water), it did not increase much. Against the background of food odor in one of the two variants, however, fish grasped more red pellets than green ones ($p < 0.05$) (variant 1) and pellets with glycine were consumed more willingly than pellets with proline (Table 3).

The introduction of skin water extract to the aquarium caused notable changes in fish behavior. The fish started to swim excitedly, made short rushes, sharply changed directions, made turns and unexpected stops, and hid in the corner of the aquarium or near the bottom 15−20 s after its introduction, and the operculum rhythm increased significantly. The response intencity to skin extract in different experiments and in different specimens varied from the weakest to the most strongly expressed reactions when, after a short agita-

Table 2. Response of the roach *Rutilus rutilus* to simultaneously introduced three agar-agar red pellets and three green pellets containing L-proline (0.1 M) or L-alanine (0.1 M) in pure water and in the presence of food odor

Type of pellets	Average number of grasps of pellets in the experimen	Consumed pellets, % of introduced	Number of experiments
Pure water			
Variant 1:			
red with proline	2.89 (52)	14.8	18
green with alanine		13.0/*	
Variant 2:			
red with alanine	3.28 (59)	31.5*/	18
green with proline		13.0	
Chironomid larvae extract, 10^{-2} g/L			
Variant 1:			
red with proline	3.25 (39)	11.1	12
green with alanine		5.6	
Variant 2:			
red with alanine	2.00 (24)	14.8	12
green with proline		13.0	

* The differences in pellet consumption are significant at $p < 0.05$; different pellets in the same variant of the experiment are before the slash, and pellets with the same amino acid in two successive variants are after the slash; the total number of grasps of all introduced pellets is in brackets.

tion and rushing about, fish hid in the corner of the aquarium and stayed motionless for a long time—from several minutes or tens of minutes after the end of the experiment. The fish demonstrated alertness for several hours; the process of feeding made them feel anxious, and the delivered live chironomid larvae were grasped unwillingly.

With skin extract, the number of grasped pellets was 2−3 times as small as in pure water. The stronger the reaction of fish to the extract of skin was, the fewer grasped pellets were registered. Even in the experiments in which notable changes in fish behavior in response to the delivery of the extract of skin were not recorded, the fish grasped pellets carefully and with a delay as compared to the experiments in pure water. If the fish response was well expressed, the fish did not catch pellets at all in such experiments. There were no significant differences between the fish response to pellets simultaneously introduced to the aquarium with respect to the number of grasps and the number of grasped and swallowed pellets. The consumption of most such pellets was low (Table 3).

The comparison of koi responses to pellets differed only in color or in composition demonstrated that in pure water, in water with chironomid larvae extract, and in water with skin extract, the fish grasped a similar number of pellets of similar color but with a different amino acid content. In some cases, however, the consumption of pellets of the same color was different. In pure water, fish consumed pellets with glycine more willingly than with proline, and the fish more willingly consumed pellets of both colors with glycine against

the background of food odor (Table 4). The number of grasps of pellets of different color but with the same amino acids was similar, except for the case in which, against the background of chironomid larvae extract, the fish showed a greater preference for red pellets than for green ones ($p = 0.018$). The consumption of pellets of different colors but having the same amino acid content was similar in pure water and in water with chironomids or skin extracts (Table 4).

Comparison of the fish responses to pellets of the same type (similar in color and composition) but under different experimental conditions demonstrated that fishes grasped the similar number of pellets, except for red pellets with glycine, in pure water and with chironomid extract ($p = 0.044$). This response parameter was significantly lower in water with skin extract as compared to pure water or water with chironomid extract for all types of pellets (Table 5). The consumption of the same pellets in pure water and with chironomid extract is similar, with exception of red pellets contained proline which were swallowed significantly worse in the water with chironomid extract. With skin extract, all pellets except green ones with glycine were consumed less than in pure water. When comparing the fish feeding in water with chironomid and with skin extracts, significant differences were found only for red pellets with glycine (Table 5).

Fish grasped more red pellets containing glycine and proline than green pellets with the same amino acids but significant differences were found only in water with food odor (Fig. 2). The consumption of all pellets with glycine (total of red and green colors) was

Table 3. Response of the koi *Cyprinus carpio* to simultaneously introduced two agar-agar red pellets and two green pellets containing L-proline (0.1 M) or glycine (0.1 M) in pure water and in the presence of food odor or alarm pheromone

Type of pellets	Grasped pellets, % of introduced	Consumed pellets, % of grasped	Average number of grasps of one pellet in the experiment, $M \pm m$			Number of experiments
			upon consumption	upon rejection	all experiments	
			Pure water			
Variant 1:						
red with proline	87.9	79.3	1.28 ± 0.10	1.42 ± 0.23	1.31 ± 0.09	33
green with glycine	78.8	88.5	1.09 ± 0.04	1.33 ± 0.33	1.12 ± 0.05	
Variant 2:						
red with glycine	85.0	84.9*/	1.18 ± 0.09	1.71 ± 0.29	1.25 ± 0.09	30
green with proline	88.3	66.7	1.03 ± 0.03	1.28 ± 0.18	1.11 ± 0.06	
			Extract of chironomid larvae, 10^{-3} g/L			
Variant 1:						
red with proline	92.3*/	52.8*/	1.05 ± 0.05/***	2.41 ± 0.24	1.69 ± 0.14*/	39
green with glycine	83.3	70.8	1.06 ± 0.04	1.42 ± 0.16	1.17 ± 0.06	
Variant 2:						
red with glycine	95.0	76.3***/	1.21 ± 0.07/*	2.0 ± 0.36	1.39 ± 0.11	40
green with proline	87.5	48.6	1.09 ± 0.05/*	1.53 ± 0.15	1.31 ± 0.08	
			Extract of skin of koi, 10^{-3} g/L			
Variant 1:						
red with proline	50.0	16.7	2.00	1.00	1.17 ± 0.17	6
green with glycine	25.0	66.7	1.00	1.00	1.00 ± 0.00	
Variant 2:						
red with glycine	42.9	20.0	1.00	1.60 ± 0.40	1.50 ± 0.34	7
green with proline	50.0	16.7	1.00	1.67 ± 0.33	1.57 ± 0.30	

The mean value of the parameter and its error; for * and ***, differences are significant at $p < 0.05$ and $p < 0.001$; those between the response to various pellets in the same variant precede the slash; those between the response to pellets upon consumption and rejection follow it.

significantly higher than the consumption of all pellets with proline in pure water and in water with chironomid extract (Fig. 3).

Monitoring of the koi response to each of the four introduced pellets made it possible to count and compare the number of grasps made by fish in cases of consumption and the rejection of pellets. It was found that, upon the consumption and rejection of pellets, fishes made a similar number of grasps of all types of pellets in pure water and in the presence of skin extract. Against the background of chironomid extract, the number of graspings upon consumption was significantly smaller than upon rejection, except for green pellets containing glycine (variant 1) (Table 3).

DISCUSSION

In fish, like in all animals, the motivational state, i.e. the predisposition or motivation to particular actions aimed at satisfying the demands (object-related need according to P.V. Simonov, 1987) is controlled by external and inner factors and can be the main reason for differences in behavioral responses to the same stimuli under similar conditions (Colgan, 1993). The defensive motivation caused by the presence of a real predator or its olfactory, visual, or other imitation changes the fish response to food items and feeding and shifts many physiological functions (Rehnberg et al., 1987; Lebedeva et al., 2000). An increase or decrease in feeding motivation is usually achieved in the experiment by alternation of feed deprivation and satiation and causes an increase or decrease, respectively, in the rate and selectivity of feeding and affects the manipulational activities of fish with food items (Ivlev, 1955; Tugendhat, 1960; Colgan, 1973; Kasumyan and Sidorov, 2010a). Even outwardly insignificant events such as swallowing or rejecting a detected and grasped small prey have notable consequences for the motivational state of the predator and strategy of its behavior. In the three-spined stickleback *Gasterosteus aculeatus*,

Table 4. Comparison of responses of koi to pellets of different types (differing in the amino acid or color) in pure water, in the presence of food odor or alarm pheromone

Compared types of pellets	Grasped pellets	Consumed pellets
	Pure water	
Red with proline/red with glycine	−	−
Green with proline/green with glycine	−	**↑
Red with proline/green with proline	−	−
Red with glycine/green with glycine	−	−
	Extract of chironomid larvae, 10^{-3} g/L	
Red with proline/red with glycine	−	**↑
Green with proline/green with glycine	−	**↑
Red with proline/green with proline	−	−
Red with glycine/green with glycine	*↓	−
	Extract of skin, 10^{-3} g/L	
Red with proline/red with glycine	−	−
Green with proline/green with glycine	−	−
Red with proline/green with proline	−	−
Red with glycine/green with glycine	−	−

* and **, differences are significant at $p < 0.05$ and $p < 0.01$; ↑ and ↓ are the higher and lower values of the response parameter, respectively, in the second of the compared samples.

Table 5. Comparison of the response of koi to pellets of the same type (similar in color and amino acid content) under different experimental conditions: in pure water and in the presence of food odor or alarm pheromone

Types of pellets	Grasped pellets	Consumed pellets
	Pure water/extract of chironomid larvae, 10^{-3} g/L	
Red with proline	−	**↓
Red with glycine	*↑	−
Green with proline	−	−
Green with glycine	−	−
	Pure water/extract of skin, 10^{-3} g/L	
Red with proline	**↓	***↓
Red with glycine	***↓	***↓
Green with proline	***↓	**↓
Green with glycine	***↓	−
	Extract of chironomid larvae, 10^{-3} g/L/extract of skin, 10^{-3} g/L	
Red with proline	***↓	−
Red with glycine	***↓	**↓
Green with proline	***↓	−
Green with glycine	***↓	−

*, ** and ***, differences are significant at $p < 0.05$ and $p < 0.01$ and $p < 0.001$; ↑ and ↓ are the higher and lower values of the response parameter, respectively, in the second of the compared samples.

one-time consumption of a small portion of food increases the rate of its subsequent searching but restricts its area (area-restricted searching), whereas, after the rejection of food items, fish rush to leave the site and temporarily decrease their searching activity (area-avoided searching) (Thomas, 1974, 1977).

The odors used in our study can affect the motivational state of fish. The alarm pheromone contained in the skin, along with a strong releasing effect, induce prolonged alertness and fear responses in fish, which are typical manifestations of the defensive motivation. Even after one instance, the effect of this natural alarm
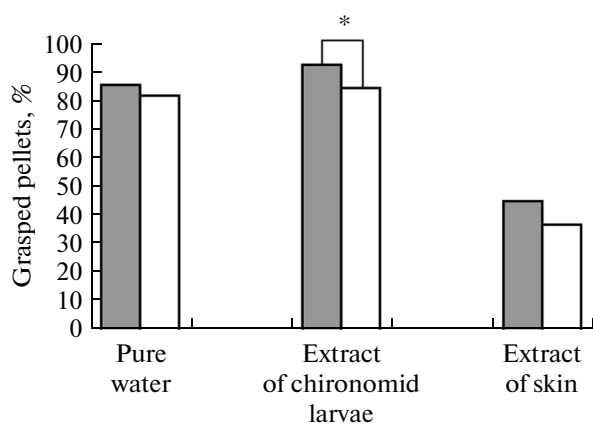
Fig. 2. Visual selection of pellets of various colors in total for pellets with different amino acids under different experimental conditions on koi. Dark columns denote red pellets with proline and glycine, and light columns denote green pellets with proline and glycine. *, differences are significant at $p < 0.05$.

Fig. 3. Taste selection of pellets with amino acids in total for pellets of various colors under different experimental conditions on koi. Dark columns denote pellets with proline of red and green color, and light columns denote pellets with glycine of red and green color. * and ***, differences are significant at $p < 0.05$ and at $p < 0.001$.

chemical signal on fish increases their anxiety and avoidance of the sites associated with the alarm pheromone, increases their intraschool contacts (Frisch, 1941; Marusov, 1976; Malyukina et al., 1977; Jachner, 1996), and causes diverse physiological abnormalities (Pfeiffer and Lamour, 1976; Pfeiffer and Riegelbauer, 1978; Pfeiffer et al., 1985), including those typical for stress (Rehnberg and Schreck, 1987; Rehnberg et al., 1987; Lebedeva et al., 1999, 2000). Food odors stimulate search and other forms of feeding agitation, and they affect collective behavior and change the responses to various external stimuli (Kasumyan and Ponomarev, 1986; Essler and Kotrschal, 1994; Carton and Montgomery, 2003; Gardiner and Atema, 2007; Barata et al., 2009). Fish perceive both chemical signals through the olfactory system (Døving et al., 2005; Kasumyan and Marusov, 2005). Their concentrations in our experiments exceeded the fish threshold sensitivity to this type of stimuli constituted 10^{-4}–10^{-5} g/L for chironomid extract and 10^{-7} g/L for skin extract (Malyukina et al., 1974; Kasumyan, 2004; Kasumyan and Marusov, 2005). In response to the skin extract, the examined fish specimens (koi) showed the defensive behavior with a typical prolonged aftereffect. However, in the presence of chironomid larvae extract, fish did not respond with searching. Search suppression can be explained by the fact that the stained pellets introduced to the aquarium at the beginning of odor stimulation were well visible and immediately grasped by fish.

Feeding motivation. The experiments demonstrated that food odor changes the motivation for feeding and stimulates food interest in potential food items. Under the effect of fish odor, fish (koi) grasp delivered pellets of any color more often than in pure water. Similar results were obtained in experiments on carp and the cod *Gadus morhua* with a similar procedure
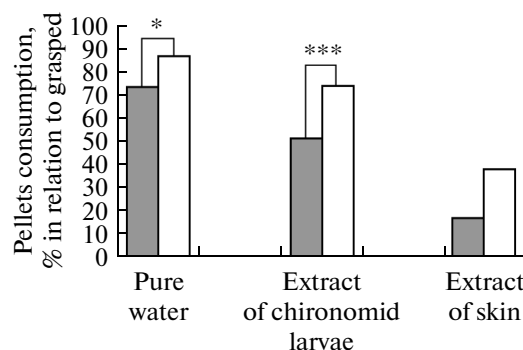
(Kasumyan et al., 2009). In addition, food odor stimulates grasping and intraoral testing, even with those items that by the size, shape and color remotely resemble food organisms (Kasumyan and Ponomarev, 1986). This explains the increase in the absolute amount of consumed food, e.g. in the gilt-head bream *Sparus auratus* and the Japanese seabream *Pagrus* (*Chrysophrys major*) upon feeding with artificial food or in combination with stimulation by natural food odors (Fuke et al., 1981; Tandler et al., 1982). Food consumption increases under the simultaneous action of food odor and visual stimuli (Kolkovski et al., 1997).

Despite the enhanced feeding motivation and increase in the absolute number of grasps of potential food items, their relative consumption decreased (Tables 3, 5). This important feature of feeding behavior is stimulated by olfactory and gustatory information, which is simultaneously received by fish and is typical, as was found before, for the response to food items with indifferent or aversive taste (Kasumyan et al., 2009). In our cases such items include pellets with proline and alanine, which are consumed less willingly than pellets with chironomid larvae extract (koi). The insufficiently attractive taste of pellets differs greatly from the highly attractive odor of a familiar food for fish, such as chironomid larvae. Under the effect of this odor, the enhanced feeding motivation results in frequent rejections of less attractive pellets and stimulates fish to search for more palatable food. As the experiments on cod and carp demonstrate, the consumption of pellets with attractive taste does not decrease against the background of food odor and remains at the same level, i.e. as it was prior odor stimulation (Kasumyan et al., 2009). The taste attractiveness of different unattractive food items decreases differently under the effect of feeding motivation, which causes shifts of taste preferences in fish. The consumption of pellets with proline and glycine by koi not only

decreases with food odor but is replaced by selective consumption of pellets with glycine only of red and green colors (Table 3).

The feeding motivation causes a stricter choice of food items, not only upon their final orosensory assessment but at earlier stages of feeding behavior. According to our data, under the effect of food odor, the fish's perception of color changes to a weak but significant preference of red pellets (Tables 3 and 4). Red color are more attractive for many fish species—the chub salmon *Oncorhynchus keta*, Atlantic salmon *Salmo salar*, rainbow trout *Oncorhynchus mykiss*, and others (Frisch, 1913; Wolf and Wales, 1953; Stradmeyer and Thorpe, 1987; Ibrahim and Huntingford, 1989; Kasumyan et al., 1992; Labas, 1992). Color preferences in fish are quickly modified in the course of acquired individual feeding experience (Clarke and Sutterlin, 1985). However, acquired habits involving food color are probably less stable, and innate color preferences begin to dominate over acquired ones upon enhanced feeding motivation. Another possible explanation of the shift in color preferences is that the used food odor was perceived by fish as not an abstraction but as a quite particular well-known food for the tested specimens—chironomid larvae. Chironomid larvae have bright red color, so their odor stimulated fish to grasp namely red pellets, which are similar in color to chironomids, from all of the various colors pellets introduced to the aquarium.

Thus, motivation stimulated by food odor not only increases the feeding activity of fish but increases their demands for food quality and food selectivity. In nature, many forage organisms are distributed unevenly and form aggregations (Kruglova and Bakanov, 1977; Greenblatt, 1982; Omori and Hamner, 1982). When swimming into the odor field formed around foraging patches, fish detect food items as a result of the search and grasp them if they have appropriate external characteristics such as size, shape, color, coloration, brightness, mobility etc. (Kistalioglu and Gibson, 1976; Pavlov and Kasumyan, 1998). However, according to our results, if a grasped food item is not of appropriate taste quality, it will be rejected after orosensory testing by fish subject to food odor agitation more probably than at a low level of food motivation. Under such conditions the fish's demands for taste quality of food become higher. Undoubtedly, the adaptive significance of such behavior is the enhancement of mechanisms responsible for food selectivity: the rejection of unattractive food items and the search of new food, which corresponds to a greater extent to food requirements and results in the detection and consumption of more palatable food items for fish. The signal field perceived by fish indicates the presence of such food items. It is known that the feeding behavior of fish has a polysensory basis. The majority of information about food items perceived via different sensory canals coincide in sign and intensity, i.e. the more coherent informational flows

are, the more effective feeding will be with respect to quality and quantity. We can suggest that an increase in the requirements for the sensory quality of food not only increases food selectivity but can decrease the risk of consuming inadequate food. The probability of grasping and swallowing of such food increases due to feeding agitation. This is confirmed, in particular, by observations of sharks, which, in the state of the so-called feeding frenzy, grasp and swallow food items that are not appropriate for feeding and threaten their health (Tester, 1963; Hart and Collin, 2015).

Defensive motivation. The effect of the alarm pheromone on the feeding behavior is different and stronger than the effect of food odor. The alarm pheromone does not increase but decreases the fish feeding motivation; fish grasp the introduced pellets several times more rarely and reject most of them. Simultaneous delivery of pellets and alarm pheromone to the aquarium results in a contradiction between feeding and defensive motivations. When they are in conflict, the defensive motivation dominates. Many experimental studies demonstrate that the fear or alertness response caused by the presence of the predator or its visual or other imitation stop or reduce the duration of fish feeding (Dill, 1983; Dill and Fraser, 1984; Fraser and Huntingford, 1986; Godin, 1986; Pitcher, 1986; Gerasimov and Linnik, 1986; Metcalfe et al., 1987; Huntingford et al., 1988; Morgan, 1988; Ibrahim and Huntingford, 1989; Milinski, 1993). This is confirmed by our results. The effect of the alarm pheromone on fish feeding has not been studied in detail, but many researchers noted a decrease or stoppage of feeding in fish in response to chemical signals of danger (Smith, 1979; Mathis and Smith, 1993; Jachner, 1995; Irving, Magurran, 1997; Jachner, Janecki, 1999; Brown et al., 2001).

Shifts in food taste or color preferences have not been found in fish subjected to alarm pheromone. The absence of such an effect is quite reasonable when fish respond to the alarm pheromone with a stoppage of feeding. Any corrections of food preferences in this case are counterproductive. It is considered that the alarm pheromone enhances visual regulation of behavior, which is important for a quick and accurately oriented locomotor response by fish to the danger signal (Pfeiffer and Riegelbauer, 1978).

Color and taste preferences in the norm. In pure water the roach and koi did not choose pellets by color; the number of grasped red and green pellets was similar in both series. It is known that the preference for food color is an innate property and is manifested in juveniles from the moment of their feeding on external food (Clarke and Sutterlin, 1985). The absence of pellet-color preferences in the roach and koi can be explained by the quick formation in tested fish of a feeding reflex for red and green pellets with chironomid larvae extract at the initial stage of experiments. No differences in taste preferences for alternative amino acids were found in the roach or koi. Hence,

according to the available data, the taste attractiveness of used amino acids is different in the studied fish specimens. It is higher for alanine than proline in the roach and is higher for proline than for glycine in the carp (Kasumyan and Morsi, 1996; Kasumyan and Nikolaeva, 2002). For the roach such differences can be caused by a significant difference in fish size; in our experiment the roach specimens were twice as large as in the earlier experiments (Kasumyan and Nikolaeva, 2002). The difference between koi and carp can be due to the long selection and breed differences of fish, because, according to electrophysiological data, the taste efficiency of amino acids differs in various fish breeds (Hara et al., 1999).

In the absence of odor stimuli, the roach and koi equally consumed pellets of various colors with the chironomid larvae extract (Table 1), which indicates a similar taste quality of the dyes used for staining agar-agar gel (Ponceau 4R and Cr_2O_3). However, we cannot disregard the differences in the taste of these dyes for fish, because their effect can be camouflaged by chironomid larvae extract in pellets. The first variant is more relevant for koi, which equally consumed pellets of various colors with the same amino acid in pure water (Tables 3, 4). However, these dyes can taste differently for roach, since, despite the equal consumption of red and green pellets with proline in pure water, the consumption of red pellets with alanine was higher than that of green pellets (Table 2).

Feeding behavior. The feeding behavior of the both species is characterized by repeated food testing; after grasping and retention in the oral cavity, the food item was rejected and grasped again after a short interval. Such repeated manipulations before swallowing or final rejection the food item are performed by many fish species. They are more typical for roach than for koi, since vision is less developed in koi, as is usually observed in benthivorous as compared to euryphagous (roach) or planktophages (Pavlovsky and Kurepina, 1953; Collin, 1999; Lisney et al., 2012). Both koi and roach have similar maniputional activity in cases when the food item is finally rejected. If it is consumed, the repeated testings are less frequent. Similar results were earlier obtained for roach and carp, though examined species differed in age and origin (Kasumyan and Sidorov, 2010c; Kasumyan and Tinkova, 2013). The similarity of results indicates the stability of behavioral stereotypes of food testing by fish. It is of interest that other fishes, such as the stone loach *Barbatula barbatula* and three-spined stickleback, in contrast to roach, koi, and carp, make more repeated graspings before swallowing than before rejection (Kasumyan and Sidorov, 2010b; Kasumyan and Mikhailova, 2014). The reasons for such behavior have not yet been elucidated. It should be emphasized that differences in the behavioral responses before food consumption or its rejection increase against the background of food odor.

CONCLUSIONS

Thus, natural odors while changing the motivational behavior of fish affect their foraging activity and selectivity at the stages of food choice and consumption. Different odors have different consequences. Food odor enhances feeding motivation, increases search activity of fish, stimulates grasping and testing of a more number of potential food items, increases food selectivity upon the choice of the food item by its external features (color) and at the stage of the final quality assessment (taste). The manifestation of stereotypes of orosensory food testing is more contrasted. Odors that warn of nearby danger (alarm pheromone) suppress feeding motivation and foraging activity but do not affect the taste preferences of fish.

According to numerous experimental studies, feeding motivation evoked in response to starvation increases foraging activity in animals and decreases their selectivity upon food choice (Ivlev, 1955; Kislalioglu and Gibson, 1976; Hughes, 1997; Gill and Hart, 1998; Reiriz et al., 1998) and consumption (Kasumyan and Sidorov, 2010a). The results demonstrate that the relationship between the change in feeding motivation and selectivity can be not reverse but direct, i.e. enhanced feeding motivation can increase instead of decrease food selectivity. The opposite effects of feeding motivation on food selectivity are probably caused by the different origins of the causes of enhanced feeding motivation in animals, which stimulate actions aimed at satisfying their food requirements. The sense of starvation evoked by feeding deprivation is an inner (endogenous) motivational factor caused by changes in the energetic metabolism of animals. These changes cause the development of unconditioned *generalized feeding motivation*, which equally increases susceptibility to food stimuli of any modality. In ectotermic animals such consequences can be caused not only by feeding deprivation but by an increase in environmental temperature as well. As is shown by our data, stimulation by food odor evokes *specialized feeding motivation*, which may be determined as *directed or purposeful*. Specialized motivation is manifested in an enhanced susceptibility to the stimuli that are, to a greater degree, associated with objects, the image of which is activated in the memory of animals by an active signal. Undoubtedly, a specialized feeding motivation can be evoked not only under effect of food odor but of food signals of any other modalities such as visual and auditory signals. The abovementioned statements are illustrated in Fig. 4.

The daily ration of fish was high in our experiments, which made it possible to consider the basic (initial) level of generalized feeding motivation in tested animals to be low. The question of how odors affect fish's feeding behavior and sensory food selection with a higher generalized feeding motivation, e.g. long-term feeding deprivation or a higher level of specialized feeding motivation affected by strong external
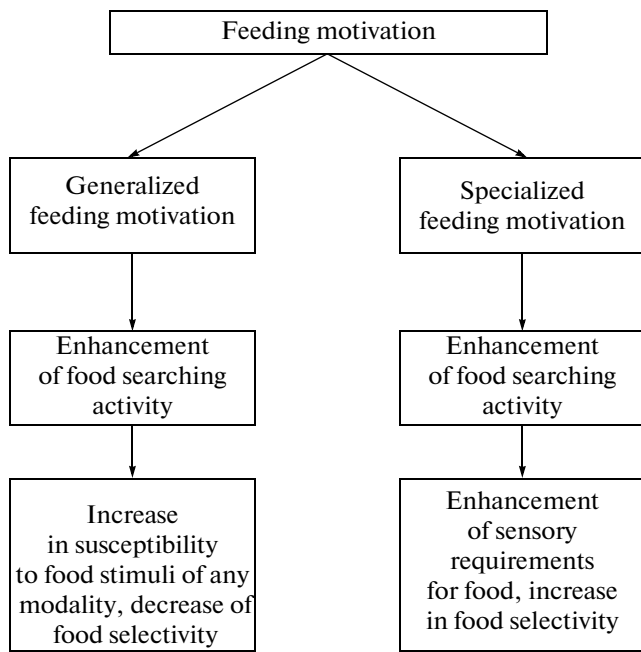
Fig. 4. Forms of feeding motivation and their effect on fish.

food stimuli, needs more detail study. We can only suggest that the food selectivity in such cases will be extremely low, as follows from the abovementioned studies on the behavior of sharks.

Animal feeding occurs under the simultaneous effect of many external factors. Most of these factors, such as odors, are able to shift the motivational status of a specimen and, as a result, change the feeding intensity and selectivity. Studies on the behavioral response to the combined effect of several stimuli of one or several modalities make it possible both to know more exactly and to predict the behavior of animals or to control it for practical purposes and to understand the mechanisms and importance of sensory integration in the manifestation of complex forms of behavior. This direction of studies aimed at the assessment and analysis of behavioral and sensory responses under multiple-factor effects has been poorly studied, not only in fish but in other animals as well (Pavlov et al., 1997; Dalton et al., 2000; New, 2002; Gardiner et al., 2014). At the same time, behavior that results from the effect of the complex combination of external factors and the inner state of animals is formed under such environmental conditions.

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