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# Individual Variability of Taste Preferences in the Minnow *Phoxinus phoxinus*

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**Abstract**—Taste preferences for the extract of Chironomidae larvae (175 g/l) and four L-amino acids (0.1 M) causing various behavioral responses (stimulating, alanine; indifferent, glutamine and proline; deterrent, phenylalanine) were determined in 49 adult minnows *Phoxinus phoxinus.* It was found that individual average consumption of the same types of food pellets, including control ones, significantly differ, and for pellets with alanine, glutamine, and chironomids extract, encompass the whole range of possible values. The difference of individual average consumption values from the group value did not exceed ±1σ standard deviation in most individuals. In 11% of cases, these average values differed by more than a factor of two. For most types of food pellets, the number of individual fish, behavioral responses of which significantly ($p < 0.05$) differed from the whole group average, did not exceed 15%, and only in the case of pellets with alanine and chironomid extract did this value reach 43 and 53%. The difference of individual average from the whole group average equally involved both increase and reduction in pellet consumption. Significant deviation of consumption of one type of pellet in certain individuals was not accompanied by similar deviations in the consumption of other types of pellets, pointing to individual patterns of taste preferences. The coefficient of variation of individual average values showed a negative correlation with the whole group average consumption of the pellets. The duration of the retention of the food pellet in the oral cavity during the first snap and during the whole experiment had relatively weaker individual variability.

Feeding is extremely diverse in fishes. The food spectra of many species include up to several dozens or even hundreds of food organisms (Martell and McClelland, 1994). The differences in feeding are especially pronounced between sympatric species (Svärdson, 1976; Sarno *et al.*, 1994; Haugen and Rygg, 1996). In addition to between-species differences, there are differences in the objects of feeding between individuals of the same species inhabiting the same water body (Allen, 1941; Smagula and Adelman, 1982; Zerba and Collins, 1992; Bridcut and Giller, 1995; Gu *et al.*, 1997; Schindler *et al.*, 1997; McLaughlin *et al.*, 1999; Beaudoin *et al.*, 1999; Vander Zanden *et al.*, 2000) or when the fish are kept in captivity (Bryan and Larkin, 1972; Ringler, 1985).

All sense organs are involved in selecting the food objects. However, the decision whether to swallow the food item or reject it is formed mainly on the basis of the information from intraoral receptors, mostly taste (Kasumyan, 1997). It is accepted that the selective consumption of the most appropriate food and the divergence of food spectra between sympatric species depends on the high species specificity of taste preferences. The significance of taste reception in these processes is supported by an absence of any significant effect of individual taste experience to the taste preferences (Kasumyan and Morsi, 1997). Regardless of the high level of genetic determinism of taste preferences, they depend on external factors, such as the water temperature and feeding motivation, affecting the immediate state of the fish and its physiological status (Kasumyan *et al.*, 1993; Kasumyan, 1997). We first obtained the data on significant individual differences (in individuals of the same age) of the carp *Cyprinus carpio* responses to the taste of stimulating substances, increasing the consumption of artificial food. This pointed to the existence in fish of individual patterns of taste preferences (Kasumyan, 2000). The aim of this paper was the assessment of individual variability of taste preferences and the behavioral response of fish to various kinds of taste substances: stimulating, deterrent, and indifferent.

## MATERIALS AND METHODS

The study was conducted on 49 adult minnows *Phoxinus phoxinus* with the average total length (TL) 6.5 cm and weight 2.2 g. The fish were caught in the Chesmena River (Moscow oblast) and, for three months before the experiments, were kept in common aquariums (100 l). Five–seven days before the experiments, the fish were transferred into individual aquariums (5 l) and trained to take artificial food pellets made of agar-agar gel (2%) and containing water extract of typical food (Chironomidae larvae). The concentration of the extract was 175 g/l. The experiments began after the training. We introduced a single pellet into the aquarium and recorded the number of snaps of the pel-

**Table 1.** Taste responses of minnows to pellets with amino acids and extract of Chironomidae ($M \pm m$)

| Stimulus | Concentration, M | Consumption of pellets, % | Index of taste attractiveness, % | Number of snaps | Retention time | | Number of experiments |
|---|---|---|---|---|---|---|---|
| | | | | | after the first snap | during the whole experiment | |
| L-alanine | 0.1 | 45.5 ± 4.5*** | 46 | 1.2 ± 0.1 | 4.5 ± 0.2*** | 4.9 ± 0.2*** | 490 |
| L-glutamine | 0.1 | 20.8 ± 3.2 | 10 | 1.1 ± 0.1 | 3.4 ± 0.2 | 3.6 ± 0.2 | 490 |
| L-proline | 0.1 | 18.2 ± 3.0 | 3 | 1.2 ± 0.1 | 3.2 ± 0.2 | 3.7 ± 0.2 | 490 |
| L-phenylalanine | 0.1 | 3.3 ± 1.2*** | –68 | 1.1 ± 0.1 | 2.1 ± 0.1*** | 2.3 ± 0.1*** | 490 |
| Chironomidae extract | 175 | 61.4 ± 4.3*** | 56 | 1.2 ± 0.1 | 4.1 ± 0.1*** | 4.6 ± 0.2** | 490 |
| Control | – | 17.1 ± 2.8 | | 1.2 ± 0.1 | 3.1 ± 0.2 | 3.5 ± 0.2 | 490 |

Note: The concentration of chironomid extract is expressed in g/l; Significance of differences from the control: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

let before it was swallowed by the fish or finally rejected. Also, we recorded the duration of the retention of the pellet in the mouth cavity after the first snap and during the whole experiment. For quantitative assessment of the taste preferences of substances contained in the pellet, we calculated the proportion (%) of swallowed pellets in the total number taken up. The cylindrical pellets (length 4.0 mm, diameter 1.35 mm) with various taste substances were given in a random sequence. The rejected pellets were removed from the aquarium immediately after the experiment. As the taste substances, we used free amino acids L-alanine, L-glutamine, L-proline, and L-phenylalanine (all in the concentration 0.1 M). Their choice was based on results of preliminary experiments. Amino acids and the extract of Chironomidae were introduced into the gel during its preparation. Also, a stain (Ponceau 4R 5 μM) was added to the gel during its preparation. The control pellets contained only the stain. The experimental procedures, fish maintenance, and preparation and keeping of pellets are described in detail elsewhere (Kasumyan and Morsi, 1996).

We conducted 10 experiments with each individual fish with all types of food pellets. The overall number of experiments was 29 400. The statistical analysis of the results included the $\chi^2$-test and the Student's *t*-test. The relationship between separate measures was assessed with the Spearman rank correlation coefficient ($r_s$). The calculation of mean values included the individual mean and the group mean, calculated on the basis of individual means. Because all individuals were tested an equal number of times, the group mean corresponded to the overall mean, obtained if all responses were collapsed into the same sample.

## RESULTS

Alanine had the most attractive taste for minnows among all amino acids used: 223 of 490 presented and taken pellets were swallowed. The consumption of pellets with alanine was almost three times higher than the control pellets, but lower than pellets with extract of Chironomidae larvae. Phenylalanine had the opposite effect: the presence of this amino acid in the pellet caused a significant reduction of its consumption. Glutamine and proline had an indifferent taste for minnows. Pellets with an attractive taste (alanine, Chironomidae extract) were retained by the fish in the mouth cavity for a longer time than control pellets or pellets with glutamine and proline. The retention time of pellets with phenylalanine was the shortest. The average number of snaps of the pellets was relatively low in experiments with all kinds of pellets (Table 1).

The range of individual mean consumption reached the maximum possible values, from 0 to 100%. This range was lower for pellets with proline, phenylalanine, and control pellets (Table 2). Out of 49 individual minnows, 16 and 25 fish showed a significant preference of alanine and Chironomidae extract, respectively. The consumption of these pellets by other individuals did not significantly differ from the consumption of control pellets. The number of fish with significant responses to pellets with glutamine and proline, indifferent for the minnow, was significantly lower, two and three, respectively. These responses, with the exception of the response to proline in one fish (minnow 6), were positive. Responses to pellets with phenylalanine was negative in six individuals. In the other 43 fish, the consumption of pellets with this amino acid did not differ significantly from the consumption of control pellets (Table 2).

The coefficient of variation of individual mean values of pellet consumption depended on the group consumption mean: the less actively the pellets were swallowed, the higher the individual variability in taste preferences to this kind of pellet (Fig. 1a). Variation of such measures of the behavioral taste response as the duration of the pellet retention in the mouth cavity after the

**Table 2.** Individual mean consumption (%) of pellets with L-alanine (0.1 M), L-glutamine (0.1 M), L-proline (0.1 M), L-phenylalanine (0.1 M), extract of Chironomidae larvae (175 g/l), and control pellets

| Individual number | Alanine | Glutamine | Proline | Phenylalanine | Chironomidae extract | Control |
|---|---|---|---|---|---|---|
| 1 | 100*** | 100*** | 60.0 ± 16.3* | 0 | 100*** | 10.0 ± 10.0 |
| 2 | 100** | 30.0 ± 15.3 | 30.0 ± 15.3 | 0* | 100* | 40.0 ± 16.3 |
| 3 | 100** | 20.0 ± 13.3 | 40.0 ± 16.3 | 20.0 ± 13.3 | 60.0 ± 16.3 | 50.0 ± 16.7 |
| 4 | 100*** | 40.0 ± 16.3 | 60.0 ± 16.3 | 10.0 ± 10.0 | 100*** | 20.0 ± 13.3 |
| 5 | 90.0 ± 10.0 | 50.0 ± 16.7 | 60.0 ± 16.3 | 0** | 100** | 50.0 ± 16.7 |
| 6 | 90.0 ± 10.0* | 30.0 ± 15.2 | 0* | 0* | 60.0 ± 16.3 | 40.0 ± 16.3 |
| 7 | 90.0 ± 10.0*** | 20.0 ± 13.3 | 60.0 ± 16.3** | 0 | 90.0 ± 10.0*** | 0 |
| 8 | 90.0 ± 10.0 | 40.0 ± 16.3 | 70.0 ± 15.3 | 10.0 ± 10.0* | 100* | 60.0 ± 16.3 |
| 9 | 80.0 ± 13.3 | 20.0 ± 13.3 | 40.0 ± 16.3 | 50.0 ± 16.7 | 40.0 ± 16.3 | 50.0 ± 16.7 |
| 10 | 80.0 ± 13.3** | 0 | 10.0 ± 10.0 | 0 | 70.0 ± 15.2* | 20.0 ± 13.3 |
| 11 | 80.0 ± 13.3** | 0 | 20.0 ± 13.3 | 10.0 ± 10.0 | 100*** | 20.0 ± 13.3 |
| 12 | 80.0 ± 13.3*** | 20.0 ± 13.3 | 10.0 ± 10.0 | 0 | 70.0 ± 15.2** | 0 |
| 13 | 70.0 ± 15.2** | 30.0 ± 15.2 | 10.0 ± 10.0 | 0 | 30.0 ± 15.3 | 10.0 ± 10.0 |
| 14 | 60.0 ± 16.3 | 40.0 ± 16.3 | 40.0 ± 16.3 | 0 | 60.0 ± 16.3 | 30.0 ± 15.2 |
| 15 | 60.0 ± 16.3 | 10.0 ± 10.0 | 0 | 0 | 30.0 ± 15.2 | 20.0 ± 13.3 |
| 16 | 50.0 ± 16.7 | 0 | 20.0 ± 13.3 | 0 | 10.0 ± 10.0 | 30.0 ± 15.2 |
| 17 | 50.0 ± 16.7 | 80.0 ± 13.3 | 50.0 ± 16.7 | 10.0 ± 10.0** | 100 | 80.0 ± 13.3 |
| 18 | 50.0 ± 16.7 | 40.0 ± 16.3 | 10.0 ± 10.0 | 10.0 ± 10.0 | 100*** | 20.0 ± 13.3 |
| 19 | 50.0 ± 16.7 | 30.0 ± 15.3 | 20.0 ± 13.3 | 0 | 70.0 ± 15.2 | 30.0 ± 15.3 |
| 20 | 50.0 ± 16.7 | 0 | 0 | 0 | 30.0 ± 15.2 | 20.0 ± 13.3 |
| 21 | 50.0 ± 16.7 | 40.0 ± 16.3 | 0 | 0 | 100*** | 20.0 ± 13.3 |
| 22 | 50.0 ± 16.7** | 10.0 ± 10.0 | 10.0 ± 10.0 | 0 | 30.0 ± 15.2 | 0 |
| 23 | 50.0 ± 16.7** | 0 | 0 | 0 | 60.0 ± 16.3* | 0 |
| 24 | 40.0 ± 16.3 | 30.0 ± 15.2 | 40.0 ± 16.3 | 10.0 ± 10.0 | 30.0 ± 15.3 | 20.0 ± 13.3 |
| 25 | 40.0 ± 16.3 | 10.0 ± 10.0 | 30.0 ± 15.3 | 10.0 ± 10.0 | 90.0 ± 10.0** | 20.0 ± 13.3 |
| 26 | 40.0 ± 16.3* | 20.0 ± 13.3 | 30.0 ± 15.3 | 0 | 40.0 ± 16.3* | 0 |
| 27 | 40.0 ± 16.3 | 0 | 10.0 ± 10.0 | 0 | 100*** | 10.0 ± 10.0 |
| 28 | 40.0 ± 16.3* | 0 | 0 | 0 | 0 | 0 |
| 29 | 40.0 ± 16.3* | 10.0 ± 10.0 | 0 | 0 | 60.0 ± 16.3** | 0 |
| 30 | 40.0 ± 16.3* | 0 | 20.0 ± 13.3 | 0 | 60.0 ± 16.3** | 0 |
| 31 | 40.0 ± 16.3 | 70.0 ± 15.3** | 20.0 ± 13.3 | 0 | 100*** | 10.0 ± 10.0 |
| 32 | 30.0 ± 15.3 | 0 | 0 | 0 | 30.0 ± 15.3 | 0 |
| 33 | 30.0 ± 15.2 | 0 | 20.0 ± 13.3 | 10.0 ± 10.0 | 20.0 ± 13.3 | 30.0 ± 15.2 |
| 34 | 30.01 ± 15.3 | 30.0 ± 15.3 | 0 | 10.0 ± 10.0 | 90.0 ± 10.0*** | 10.0 ± 10.0 |
| 35 | 20.0 ± 13.3 | 10.0 ± 10.0 | 10.0 ± 10.0 | 0 | 20.0 ± 13.3 | 0 |
| 36 | 20.0 ± 13.3 | 30.0 ± 15.3 | 0 | 0 | 60.0 ± 16.3 | 20.0 ± 13.3 |
| 37 | 20.0 ± 13.3 | 30.0 ± 15.3 | 0 | 0 | 40.0 ± 16.3 | 10.0 ± 10.0 |
| 38 | 20.0 ± 13.3 | 0 | 0 | 0 | 60.0 ± 15.2** | 0 |
| 39 | 20.0 ± 13.3 | 10.0 ± 10.0 | 0 | 0 | 60.0 ± 16.3** | 0 |
| 40 | 20.0 ± 13.3 | 50.0 ± 16.7 | 60.0 ± 16.3 | 0 | 60.0 ± 16.3 | 20.0 ± 13.3 |
| 41 | 10.0 ± 10.0 | 10.0 ± 10.0 | 0 | 0 | 30.0 ± 15.2 | 0 |
| 42 | 10.0 ± 10.0 | 20.0 ± 13.3 | 10.0 ± 10.0 | 0** | 80.0 ± 13.3 | 50.0 ± 16.7 |
| 43 | 10.0 ± 10.0 | 30.0 ± 15.3 | 0 | 0 | 100*** | 0 |
| 44 | 0 | 0 | 10.0 ± 10.0 | 0 | 50.0 ± 16.6 | 20.0 ± 13.3 |
| 45 | 0 | 0 | 0 | 0 | 60.0 ± 16.3** | 0 |
| 46 | 0 | 0 | 0 | 0 | 10.0 ± 10.0 | 0 |
| 47 | 0 | 10.0 ± 10.0 | 10.0 ± 10.0 | 0 | 20.0 ± 13.3 | 0 |
| 48 | 0 | 0 | 0 | 0 | 70.0 ± 15.3** | 0 |
| 49 | 0 | 0 | 0 | 0 | 60.0 ± 16.3** | 0 |
| *M* ± *m* | 45.5 ± 4.5 | 20.8 ± 3.2 | 18.2 ± 3.2 | 3.3 ± 1.2 | 61.4 ± 4.3 | 17.1 ± 2.8 |
| Variation range | 0–100 | 0–100 | 0–70 | 0–50 | 0–100 | 0–80 |
| σ | 31.2 | 22.2 | 21.2 | 8.3 | 30.1 | 19.3 |
| *CV*, % | 68.6 | 108.2 | 117.2 | 253.1 | 49.1 | 112.3 |

Note: *M* ± *m*, arithmetic mean of individual means (group mean) and its standard error; σ, standard deviation; *CV*, coefficient of variation; Significance of differences with respect to the responses of the fish to control stimuli: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

**Table 3.** Individual mean retention time (s) of pellets with L-alanine (0.1 M), L-glutamine (0.1 M), L-proline (0.1 M), L-phenylalanine (0.1 M), extract of Chironomidae larvae (175 g/l), and control pellets after the first snap

| Individual number | Alanine | Glutamine | Proline | Phenylalanine | Chironomidae extract | Control |
|---|---|---|---|---|---|---|
| 1 | 5.2 ± 0.4 | 5.1 ± 0.5 | 4.6 ± 0.7 | 2.0 ± 0.2*** | 3.3 ± 0.3* | 5.3 ± 0.7 |
| 2 | 6.0 ± 0.6* | 3.9 ± 0.7 | 3.6 ± 0.6 | 1.7 ± 0.4 | 4.4 ± 0.3 | 3.6 ± 0.9 |
| 3 | 6.2 ± 0.5* | 4.7 ± 0.9 | 4.4 ± 0.7 | 3.8 ± 0.7 | 4.0 ± 0.5 | 4.4 ± 0.5 |
| 4 | 5.9 ± 1.0** | 5.7 ± 0.8*** | 5.8 ± 0.8*** | 3.3 ± 0.5* | 3.0 ± 0.3* | 1.8 ± 0.3 |
| 5 | 6.9 ± 0.6* | 6.2 ± 1.1 | 4.5 ± 0.7 | 1.3 ± 0.2*** | 4.8 ± 0.6 | 4.6 ± 0.8 |
| 6 | 6.2 ± 0.7* | 3.1 ± 0.5 | 2.3 ± 0.3** | 2.3 ± 0.3** | 5.0 ± 0.8 | 4.2 ± 0.5 |
| 7 | 7.3 ± 1.2** | 4.9 ± 1.1* | 4.6 ± 0.8* | 3.4 ± 0.8 | 4.6 ± 0.6** | 2.4 ± 0.4 |
| 8 | 5.6 ± 0.5 | 5.3 ± 0.9 | 6.5 ± 1.0 | 4.2 ± 0.9 | 4.7 ± 0.4 | 6.6 ± 1.0 |
| 9 | 6.4 ± 0.6 | 3.9 ± 0.6 | 5.0 ± 0.9 | 4.7 ± 0.7 | 3.6 ± 0.3* | 5.8 ± 0.8 |
| 10 | 5.5 ± 0.5 | 3.2 ± 0.3 | 2.8 ± 0.4 | 1.9 ± 0.2* | 2.3 ± 0.2* | 4.0 ± 0.7 |
| 11 | 7.1 ± 0.9* | 1.8 ± 0.2 | 3.1 ± 0.4 | 1.8 ± 0.5 | 4.7 ± 0.5 | 3.3 ± 1.1 |
| 12 | 5.9 ± 0.8*** | 3.9 ± 0.6** | 4.1 ± 0.8** | 1.9 ± 0.2 | 4.1 ± 0.5** | 1.7 ± 0.3 |
| 13 | 4.5 ± 0.8* | 3.2 ± 0.9 | 2.6 ± 0.3 | 1.5 ± 0.3 | 4.1 ± 0.7 | 2.3 ± 0.5 |
| 14 | 4.8 ± 0.5* | 3.7 ± 0.9 | 3.6 ± 0.8 | 1.4 ± 0.3* | 3.2 ± 0.4 | 2.9 ± 0.6 |
| 15 | 6.5 ± 0.9* | 3.5 ± 0.8 | 1.7 ± 0.3** | 2.7 ± 0.5 | 4.0 ± 0.6 | 3.8 ± 0.7 |
| 16 | 5.2 ± 0.7*** | 1.6 ± 0.2 | 2.5 ± 0.4* | 1.8 ± 0.2 | 3.3 ± 0.4 | 2.9 ± 0.6 |
| 17 | 4.7 ± 1.1* | 5.5 ± 0.8* | 5.7 ± 1.3 | 3.3 ± 0.5*** | 3.2 ± 0.2*** | 9.0 ± 1.2 |
| 18 | 6.0 ± 0.8* | 4.6 ± 0.6 | 3.0 ± 0.7 | 3.3 ± 1.0 | 3.6 ± 0.4 | 3.5 ± 0.7 |
| 19 | 3.9 ± 0.6 | 5.3 ± 0.6 | 3.6 ± 0.6 | 1.1 ± 0.2*** | 4.6 ± 0.3 | 4.9 ± 0.6 |
| 20 | 4.3 ± 0.9 | 1.7 ± 0.2* | 2.3 ± 0.6 | 1.7 ± 0.2* | 2.3 ± 0.4 | 4.2 ± 0.9 |
| 21 | 5.0 ± 0.7 | 4.7 ± 0.8 | 3.1 ± 0.3 | 2.3 ± 0.4 | 4.7 ± 0.4 | 3.7 ± 0.6 |
| 22 | 5.2 ± 0.7*** | 2.6 ± 0.4 | 2.9 ± 0.7 | 3.1 ± 0.7 | 3.7 ± 0.5** | 1.9 ± 0.2 |
| 23 | 4.1 ± 0.9 | 1.7 ± 0.5 | 2.5 ± 0.4 | 1.9 ± 0.2 | 5.2 ± 0.5*** | 2.4 ± 0.3 |
| 24 | 3.5 ± 0.5 | 2.9 ± 0.5 | 4.2 ± 0.8 | 2.0 ± 0.6 | 3.7 ± 0.2 | 3.5 ± 0.5 |
| 25 | 2.9 ± 0.5 | 2.7 ± 0.4 | 3.9 ± 0.5 | 2.2 ± 0.8 | 2.7 ± 0.2 | 3.3 ± 0.4 |
| 26 | 3.1 ± 0.6* | 3.5 ± 0.9 | 3.6 ± 0.7* | 1.8 ± 0.3 | 4.9 ± 0.7*** | 1.5 ± 0.3 |
| 27 | 3.3 ± 0.5 | 2.6 ± 0.4 | 2.8 ± 0.5 | 1.5 ± 0.2 | 4.9 ± 0.5* | 2.3 ± 0.9 |
| 28 | 3.6 ± 0.7 | 1.7 ± 0.2 | 2.3 ± 0.3 | 1.5 ± 0.1 | 2.2 ± 0.4* | 2.3 ± 0.4 |
| 29 | 3.6 ± 0.7* | 3.0 ± 0.8 | 2.4 ± 0.2 | 1.4 ± 0.2 | 4.0 ± 0.3*** | 1.8 ± 0.4 |
| 30 | 3.8 ± 0.6*** | 2.4 ± 0.2** | 2.4 ± 0.4* | 1.6 ± 0.1 | 5.8 ± 1.2** | 1.4 ± 0.1 |
| 31 | 4.6 ± 0.9 | 5.1 ± 1.2 | 2.9 ± 0.6 | 3.0 ± 0.4 | 5.5 ± 0.4** | 3.0 ± 0.5 |
| 32 | 4.5 ± 0.9** | 3.5 ± 0.4*** | 3.1 ± 0.2*** | 1.2 ± 0.2 | 3.9 ± 0.7** | 1.6 ± 0.1 |
| 33 | 4.7 ± 0.8 | 1.9 ± 0.3** | 3.6 ± 1.0 | 1.7 ± 0.3*** | 3.7 ± 0.5 | 5.0 ± 0.8 |
| 34 | 3.8 ± 0.9 | 3.9 ± 1.1 | 2.3 ± 0.2 | 2.3 ± 0.5 | 4.2 ± 0.4* | 2.2 ± 0.7 |
| 35 | 4.0 ± 0.8** | 2.7 ± 0.6 | 3.1 ± 0.8 | 1.4 ± 0.2 | 4.7 ± 0.8** | 1.4 ± 0.2 |
| 36 | 3.6 ± 1.3 | 2.1 ± 0.4 | 2.5 ± 0.3 | 2.1 ± 0.3 | 4.9 ± 0.6** | 2.7 ± 0.5 |
| 37 | 4.8 ± 1.0 | 4.9 ± 0.9 | 1.8 ± 0.3 | 1.8 ± 0.3 | 4.2 ± 0.7 | 3.4 ± 0.7 |
| 38 | 3.8 ± 0.6** | 2.4 ± 0.3 | 1.9 ± 0.2 | 1.8 ± 0.1 | 6.0 ± 1.0*** | 1.6 ± 0.2 |
| 39 | 2.8 ± 0.5* | 2.2 ± 0.4 | 2.4 ± 0.5 | 1.5 ± 0.2 | 3.1 ± 0.5* | 1.7 ± 0.2 |
| 40 | 3.4 ± 0.4 | 4.2 ± 0.6 | 5.1 ± 0.8* | 1.2 ± 0.1*** | 4.8 ± 0.9 | 3.1 ± 0.3 |
| 41 | 3.2 ± 0.7* | 3.4 ± 0.8* | 2.3 ± 0.7 | 1.5 ± 0.2 | 4.8 ± 0.9** | 1.4 ± 0.1 |
| 42 | 3.5 ± 0.9 | 3.0 ± 0.8 | 3.4 ± 0.8 | 1.9 ± 0.3* | 4.6 ± 0.7 | 5.9 ± 1.5 |
| 43 | 3.3 ± 0.8 | 3.8 ± 0.9 | 2.8 ± 0.8 | 3.0 ± 0.8 | 3.2 ± 0.2 | 2.3 ± 0.5 |
| 44 | 2.1 ± 0.3 | 2.1 ± 0.3 | 2.4 ± 0.5 | 2.1 ± 0.4 | 5.9 ± 0.3** | 3.3 ± 0.7 |
| 45 | 3.7 ± 0.3 | 2.6 ± 0.3 | 2.3 ± 0.2 | 1.4 ± 0.1*** | 4.6 ± 0.5** | 2.8 ± 0.3 |
| 46 | 2.1 ± 0.2 | 1.8 ± 0.2 | 1.4 ± 0.2 | 1.1 ± 0.1* | 2.0 ± 0.2 | 1.8 ± 0.2 |
| 47 | 2.2 ± 0.3 | 2.8 ± 0.8 | 3.4 ± 0.4 | 1.7 ± 0.2 | 3.2 ± 0.5 | 2.4 ± 0.3 |
| 48 | 2.8 ± 0.5 | 1.8 ± 0.2 | 2.6 ± 0.4 | 1.4 ± 0.2 | 5.9 ± 1.1** | 2.1 ± 0.4 |
| 49 | 3.3 ± 0.8 | 1.7 ± 0.5 | 3.3 ± 0.6 | 1.4 ± 0.1* | 5.0 ± 0.8* | 2.5 ± 0.4 |
| *M* ± *m* | 4.5 ± 0.2 | 3.4 ± 0.2 | 3.3 ± 0.2 | 2.1 ± 0.1 | 4.1 ± 0.1 | 3.2 ± 0.2 |
| Variation range | 2.1–7.3 | 1.6–6.2 | 1.4–6.5 | 1.1–4.7 | 2.0–6.0 | 1.4–9.0 |
| σ | 1.4 | 1.3 | 1.1 | 0.9 | 0.9 | 1.6 |
| *CV*, % | 30.4 | 37.8 | 34.6 | 41.0 | 24.1 | 49.7 |

Note: see note to Table 2.

**Table 4.** Individual mean retention time (s) of pellets with L-alanine (0.1 M), L-glutamine (0.1 M), L-proline (0.1 M), L-phenylalanine (0.1 M), extract of Chironomidae larvae (175 g/l), and control pellets for the whole experiment

| Individual number | Alanine | Glutamine | Proline | Phenylalanine | Chironomidae extract | Control |
|---|---|---|---|---|---|---|
| 1 | 5.2 ± 0.4 | 5.1 ± 0.5 | 4.8 ± 0.7 | 2.2 ± 0.3** | 3.3 ± 0.3* | 5.4 ± 0.8 |
| 2 | 6.0 ± 0.6 | 4.2 ± 0.7 | 4.3 ± 0.7 | 1.8 ± 0.5* | 4.5 ± 0.3 | 6.0 ± 1.5 |
| 3 | 6.2 ± 0.5 | 4.9 ± 1.0 | 4.7 ± 0.7 | 5.3 ± 1.3 | 4.0 ± 0.5 | 4.8 ± 0.6 |
| 4 | 8.0 ± 0.6*** | 5.9 ± 0.7** | 6.6 ± 0.8*** | 4.2 ± 0.8 | 3.0 ± 0.3 | 2.8 ± 0.6 |
| 5 | 6.9 ± 0.6 | 6.2 ± 1.1 | 5.3 ± 0.6 | 1.3 ± 0.1*** | 4.9 ± 0.7 | 5.8 ± 0.7 |
| 6 | 6.4 ± 0.8* | 4.7 ± 0.9 | 2.5 ± 0.3** | 2.5 ± 0.3* | 6.1 ± 0.8 | 4.2 ± 0.5 |
| 7 | 7.5 ± 1.1* | 5.7 ± 1.2 | 5.3 ± 0.8 | 3.5 ± 0.9 | 5.0 ± 0.7 | 3.9 ± 0.7 |
| 8 | 6.2 ± 0.2 | 6.3 ± 0.9 | 7.5 ± 1.1 | 4.8 ± 0.9* | 4.7 ± 0.4** | 7.7 ± 0.7 |
| 9 | 6.4 ± 0.6 | 3.9 ± 0.6 | 6.0 ± 0.9 | 4.7 ± 0.7 | 3.9 ± 0.3* | 5.8 ± 0.8 |
| 10 | 5.8 ± 0.5 | 3.2 ± 0.3 | 4.9 ± 1.4 | 2.0 ± 0.3* | 2.5 ± 0.2 | 4.0 ± 0.7 |
| 11 | 7.2 ± 1.0 | 2.7 ± 0.6 | 4.4 ± 0.7 | 2.2 ± 0.5 | 4.7 ± 0.5 | 4.3 ± 1.1 |
| 12 | 6.9 ± 0.8* | 4.5 ± 0.7 | 5.6 ± 0.8 | 2.0 ± 0.3 | 4.1 ± 0.5** | 3.3 ± 1.0 |
| 13 | 6.1 ± 0.5* | 4.2 ± 0.8 | 3.4 ± 0.6 | 1.5 ± 0.3 | 4.7 ± 0.7 | 3.5 ± 1.0 |
| 14 | 4.8 ± 0.5* | 4.1 ± 0.9 | 5.8 ± 1.1 | 2.2 ± 0.4 | 3.6 ± 0.4 | 3.3 ± 0.6 |
| 15 | 6.8 ± 0.8 | 3.5 ± 0.8 | 1.7 ± 0.3* | 2.7 ± 0.5 | 4.7 ± 0.6 | 4.5 ± 1.0 |
| 16 | 5.2 ± 0.7** | 1.6 ± 0.2* | 2.6 ± 0.3 | 1.8 ± 0.2 | 3.3 ± 0.4 | 3.3 ± 0.6 |
| 17 | 4.7 ± 1.1* | 5.5 ± 0.8* | 6.4 ± 1.2 | 3.8 ± 0.8** | 3.2 ± 0.2*** | 9.0 ± 1.2 |
| 18 | 6.0 ± 0.8 | 4.6 ± 0.6 | 3.0 ± 0.7 | 3.3 ± 1.0 | 3.6 ± 0.4 | 4.1 ± 0.9 |
| 19 | 4.3 ± 0.5 | 5.3 ± 0.6 | 3.6 ± 0.6 | 1.1 ± 0.2*** | 4.6 ± 0.3 | 5.1 ± 0.6 |
| 20 | 4.5 ± 0.8 | 1.7 ± 0.2* | 2.3 ± 0.6 | 1.7 ± 0.2* | 3.7 ± 0.7 | 4.2 ± 0.9 |
| 21 | 5.1 ± 0.7 | 4.7 ± 0.8 | 3.1 ± 0.3 | 2.3 ± 0.4 | 4.7 ± 0.4 | 3.7 ± 0.6 |
| 22 | 5.5 ± 0.6*** | 2.6 ± 0.4 | 3.3 ± 0.9 | 3.3 ± 0.8 | 4.0 ± 0.4*** | 2.1 ± 0.2 |
| 23 | 6.1 ± 0.8*** | 1.7 ± 0.5 | 2.8 ± 0.3 | 1.9 ± 0.2 | 6.4 ± 0.3*** | 2.4 ± 0.3 |
| 24 | 3.5 ± 0.5 | 3.6 ± 0.6 | 4.6 ± 0.7 | 2.0 ± 0.6 | 3.7 ± 0.2 | 3.7 ± 0.6 |
| 25 | 3.0 ± 0.5 | 3.4 ± 0.4 | 4.1 ± 0.5 | 2.4 ± 0.8 | 2.7 ± 0.2** | 4.4 ± 0.5 |
| 26 | 3.6 ± 0.8* | 3.5 ± 0.9 | 4.0 ± 0.6** | 1.8 ± 0.3 | 4.9 ± 0.7*** | 1.5 ± 0.3 |
| 27 | 3.5 ± 0.5 | 3.2 ± 0.7 | 2.8 ± 0.5 | 1.5 ± 0.2 | 4.9 ± 0.5* | 2.3 ± 0.9 |
| 28 | 4.4 ± 0.5** | 2.1 ± 0.2 | 2.3 ± 0.3 | 1.5 ± 0.1 | 3.4 ± 0.7 | 2.3 ± 0.4 |
| 29 | 4.4 ± 0.5** | 3.0 ± 0.8 | 2.4 ± 0.2 | 1.4 ± 0.2 | 4.3 ± 0.3*** | 1.8 ± 0.4 |
| 30 | 5.0 ± 0.6*** | 2.4 ± 0.2** | 2.6 ± 0.4* | 1.6 ± 0.1 | 6.4 ± 1.0*** | 1.4 ± 0.1 |
| 31 | 5.5 ± 0.8* | 5.3 ± 1.1 | 4.1 ± 0.7 | 3.0 ± 0.4 | 5.5 ± 0.4** | 3.1 ± 0.5 |
| 32 | 4.5 ± 0.9** | 3.5 ± 0.4*** | 3.1 ± 0.2*** | 1.2 ± 0.2 | 4.4 ± 0.7** | 1.6 ± 0.1 |
| 33 | 4.7 ± 0.8 | 1.9 ± 0.3** | 4.2 ± 1.0 | 2.2 ± 0.4** | 3.7 ± 0.5 | 5.0 ± 0.8 |
| 34 | 4.2 ± 1.0 | 4.2 ± 1.1 | 2.5 ± 0.2 | 2.3 ± 0.5 | 4.3 ± 0.3* | 2.7 ± 0.7 |
| 35 | 4.0 ± 0.8** | 2.7 ± 0.6 | 3.1 ± 0.8 | 1.4 ± 0.2 | 4.9 ± 0.8*** | 1.4 ± 0.2 |
| 36 | 3.9 ± 1.2 | 3.5 ± 1.0 | 2.5 ± 0.3 | 2.1 ± 0.3 | 5.4 ± 0.4** | 3.2 ± 0.5 |
| 37 | 5.5 ± 1.0 | 4.9 ± 0.9 | 1.8 ± 0.3 | 2.2 ± 0.5 | 4.2 ± 0.7 | 3.4 ± 0.7 |
| 38 | 4.6 ± 0.8** | 2.5 ± 0.4 | 1.9 ± 0.2 | 1.8 ± 0.1 | 6.9 ± 0.8*** | 1.6 ± 0.2 |
| 39 | 3.4 ± 0.6* | 2.2 ± 0.4 | 2.6 ± 0.5 | 2.2 ± 0.2 | 5.9 ± 0.8*** | 1.8 ± 0.2 |
| 40 | 4.9 ± 0.8 | 5.0 ± 0.6 | 6.7 ± 1.0* | 1.2 ± 0.1*** | 5.4 ± 0.7 | 3.7 ± 0.4 |
| 41 | 3.3 ± 0.7* | 3.5 ± 0.7* | 2.4 ± 0.7 | 1.5 ± 0.2 | 5.6 ± 0.7*** | 1.4 ± 0.1 |
| 42 | 3.6 ± 0.8 | 3.0 ± 0.8* | 3.5 ± 0.8 | 2.6 ± 0.7* | 5.4 ± 0.4 | 7.0 ± 1.6 |
| 43 | 4.5 ± 0.7* | 3.9 ± 0.9 | 3.1 ± 0.8 | 3.2 ± 0.9 | 3.2 ± 0.2 | 2.3 ± 0.5 |
| 44 | 2.1 ± 0.3 | 2.3 ± 0.4 | 2.4 ± 0.5 | 2.1 ± 0.4 | 5.9 ± 0.3** | 3.3 ± 0.7 |
| 45 | 3.7 ± 0.3 | 2.6 ± 0.3 | 2.3 ± 0.2 | 1.4 ± 0.1*** | 4.7 ± 0.5** | 3.0 ± 0.3 |
| 46 | 2.1 ± 0.2 | 1.8 ± 0.2 | 1.4 ± 0.2 | 1.1 ± 0.1* | 2.6 ± 0.4 | 2.3 ± 0.5 |
| 47 | 2.6 ± 0.4 | 2.8 ± 0.8 | 7.1 ± 2.8 | 1.7 ± 0.2 | 3.8 ± 0.5* | 2.4 ± 0.3 |
| 48 | 3.4 ± 0.7 | 1.8 ± 0.2 | 2.6 ± 0.4 | 1.4 ± 0.2 | 7.4 ± 0.8*** | 2.2 ± 0.4 |
| 49 | 5.1 ± 1.0* | 1.7 ± 0.5 | 3.4 ± 0.6 | 1.4 ± 0.1* | 6.4 ± 0.6*** | 2.5 ± 0.4 |
| *M* ± *m* | 4.9 ± 0.2 | 3.6 ± 0.2 | 3.7 ± 0.2 | 2.3 ± 0.2 | 4.6 ± 0.2 | 3.6 ± 0.2 |
| Variation range | 2.1–8.0 | 1.6–6.3 | 1.4–7.5 | 1.1–5.3 | 2.6–7.4 | 1.4–9.0 |
| $\sigma$ | 1.4 | 1.3 | 1.5 | 1.0 | 1.1 | 1.7 |
| *CV*, % | 28.2 | 36.7 | 41.4 | 44.6 | 24.9 | 47.6 |

Note: See Note to Table 2.

**Table 5.** Individual mean number of snaps of pellets with L-alanine (0.1 M), L-glutamine (0.1 M), L-proline (0.1 M), L-phenylalanine (0.1 M), extract of Chironomidae larvae (175 g/l), and control pellets

| Individual number | Alanine | Glutamine | Proline | Phenylalanine | Chironomidae extract | Control |
|---|---|---|---|---|---|---|
| 1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.2 ± 0.1 | 1.0 ± 0.0 | 1.1 ± 0.1 |
| 2 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.3 ± 0.3 | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.7 ± 0.3 |
| 3 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.3 ± 0.3 | 1.0 ± 0.0 | 1.1 ± 0.1 |
| 4 | 1.6 ± 0.2 | 1.3 ± 0.2 | 1.4 ± 0.2 | 1.2 ± 0.1 | 1.0 ± 0.0 | 1.3 ± 0.2 |
| 5 | 1.0 ± 0.0 | 1.0 ± 0.0* | 1.2 ± 0.1 | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.6 ± 0.3 |
| 6 | 1.1 ± 0.1 | 1.7 ± 0.3* | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.5 ± 0.3 | 1.0 ± 0.0 |
| 7 | 1.1 ± 0.1 | 1.4 ± 0.3 | 1.3 ± 0.3 | 1.1 ± 0.1 | 1.2 ± 0.1 | 1.7 ± 0.3 |
| 8 | 1.3 ± 0.3 | 1.5 ± 0.2 | 1.2 ± 0.1 | 1.3 ± 0.2 | 1.0 ± 0.0 | 1.4 ± 0.2 |
| 9 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.2 ± 0.1 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.0 ± 0.0 |
| 10 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.5 ± 0.3* | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.0 ± 0.0 |
| 11 | 1.1 ± 0.1 | 1.5 ± 0.3 | 1.8 ± 0.3 | 1.2 ± 0.1 | 1.0 ± 0.0 | 1.4 ± 0.2 |
| 12 | 1.4 ± 0.2 | 1.5 ± 0.3 | 2.0 ± 0.4 | 1.1 ± 0.1 | 1.0 ± 0.1* | 1.9 ± 0.5 |
| 13 | 1.5 ± 0.2 | 1.5 ± 0.3 | 1.3 ± 0.2 | 1.0 ± 0.0 | 1.2 ± 0.1 | 1.4 ± 0.3 |
| 14 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.8 ± 0.4 | 1.6 ± 0.3 | 1.1 ± 0.1 | 1.2 ± 0.1 |
| 15 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.2 ± 0.1 | 1.1 ± 0.1 |
| 16 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.2 ± 0.1 |
| 17 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.2 ± 0.1 | 1.2 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 |
| 18 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 |
| 19 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 |
| 20 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.4 ± 0.2 | 1.0 ± 0.0 |
| 21 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 |
| 22 | 1.3 ± 0.2 | 1.0 ± 0.0 | 1.2 ± 0.1 | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.1 ± 0.1 |
| 23 | 1.6 ± 0.3 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.3 ± 0.2 | 1.0 ± 0.0 |
| 24 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 |
| 25 | 1.1 ± 0.1 | 1.4 ± 0.3 | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.6 ± 0.3 |
| 26 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 |
| 27 | 1.1 ± 0.1 | 1.3 ± 0.2 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 |
| 28 | 1.5 ± 0.2 | 1.3 ± 0.2 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.5 ± 0.3 | 1.0 ± 0.0 |
| 29 | 1.5 ± 0.2 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.0 ± 0.0 |
| 30 | 1.7 ± 0.3* | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.3 ± 0.2 | 1.0 ± 0.0 |
| 31 | 1.7 ± 0.3 | 1.1 ± 0.1 | 1.5 ± 0.2 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 |
| 32 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.2 ± 0.1 | 1.0 ± 0.0 |
| 33 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.2 ± 0.1 | 1.2 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 |
| 34 | 1.1 ± 0.1 | 1.2 ± 0.1 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.3 ± 0.2 |
| 35 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.0 ± 0.0 |
| 36 | 1.1 ± 0.1 | 1.4 ± 0.3 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.2 ± 0.2 | 1.3 ± 0.3 |
| 37 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.2 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 |
| 38 | 1.3 ± 0.3 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.3 ± 0.2 | 1.0 ± 0.0 |
| 39 | 1.5 ± 0.3 | 1.0 ± 0.0 | 1.2 ± 0.1 | 1.4 ± 0.2 | 2.3 ± 0.5* | 1.1 ± 0.1 |
| 40 | 1.5 ± 0.3 | 1.4 ± 0.3 | 1.4 ± 0.3 | 1.0 ± 0.0 | 1.4 ± 0.3 | 1.3 ± 0.2 |
| 41 | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.5 ± 0.3 | 1.0 ± 0.0 |
| 42 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.2 ± 0.1 | 1.2 ± 0.1 | 1.2 ± 0.1 |
| 43 | 2.1 ± 0.4* | 1.1 ± 0.1 | 1.3 ± 0.2 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.1 ± 0.1 |
| 44 | 1.0 ± 0.0 | 1.3 ± 0.2 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 |
| 45 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.1 ± 0.1 |
| 46 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.4 ± 0.2 | 1.5 ± 0.4 |
| 47 | 1.2 ± 0.1 | 1.0 ± 0.0 | 1.3 ± 0.2 | 1.0 ± 0.0 | 1.3 ± 0.2 | 1.0 ± 0.0 |
| 48 | 1.5 ± 0.3 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.6 ± 0.3 | 1.1 ± 0.1 |
| 49 | 1.5 ± 0.2 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.0 ± 0.0 | 1.5 ± 0.2* | 1.0 ± 0.0 |
| $M \pm m$ | 1.2 ± 0.04 | 1.1 ± 0.03 | 1.2 ± 0.03 | 1.1 ± 0.02 | 1.2 ± 0.03 | 1.2 ± 0.03 |
| Variation range | 1.0–2.1 | 1.0–1.7 | 1.0–2.0 | 1.0–2.1 | 1.0–2.3 | 1.0–1.9 |
| σ | 0.3 | 0.2 | 0.2 | 0.1 | 0.2 | 0.2 |
| *CV*, % | 20.9 | 16.8 | 19.2 | 11.4 | 20.4 | 19.6 |

Note: See Note to Table 2.

first snap and during the total experiment was significantly lower than the consumption of pellets (Tables 3 and 4). The dependence of the variation of these measures on the taste attractiveness of the substance had the same pattern (Fig. 1b). The coefficients of variation of the number of snaps ranged for pellets of various kinds in a narrow interval from 11.4 to 20.9 and had no relation with the taste attractiveness of the substance (Table 5).

Correlation analysis in most cases revealed a significant positive relationship between the consumption of various kinds of pellets by the fish (Table 6). However, the responses of certain individuals to certain substances could differ drastically. For example, the consumption of pellets with glutamine and chironomid extract by minnow 31 was, respectively, three and two times higher than the group mean, whereas the consumption of pellets with alanine, proline, phenylalanine, and control pellets did not differ significantly from the group mean. The high preference of alanine, proline, and chironomid extract by minnow 7 (2, 3, and 1.5 times higher than the group mean) was accompanied by a reduced consumption of control pellets or close to the group average consumption of pellets with glutamine and phenylalanine. The inconsistent consumption of various kinds of pellets was characteristic of many other individual minnows (Table 2). Individual differences in the responding of the fish to pellets were conspicuous also during the analysis of the data on the retention time and the number of snaps (Tables 3–5).

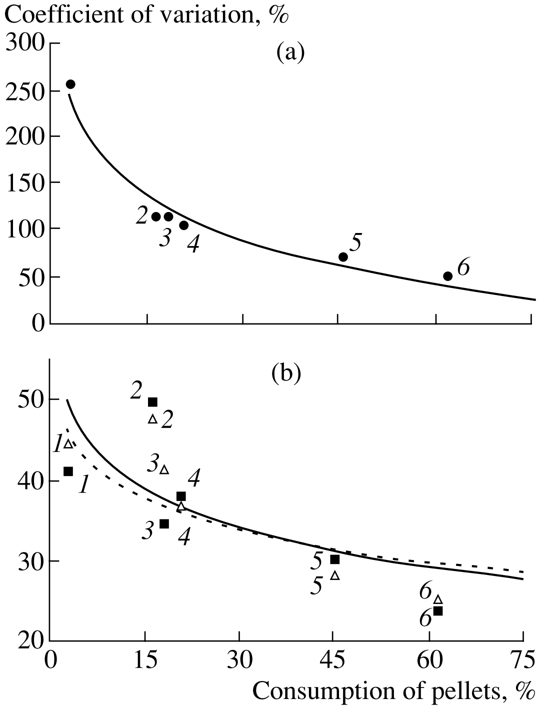

**Fig. 1.** The relationships between the coefficient of variation of the (a) consumption and (b) retention time of pellets and their taste attractiveness. Solid line and squares are the retention time of the pellet during the whole experiment. Broken line and triangles are the retention time at the first snap. (1) phenylalanine; (2) control pellets; (3) L-proline; (4) L-glutamine; (5) L-alanine; (6) Chironomidae extract.

For quantitative assessment of the proportion of fish which deviate in their taste preferences, we counted the number of fish in which the consumption of pellets differs from the group mean by multiple standard deviations (because of certain characteristics of the data distribution, we did not conduct such computations for phenylalanine) (Table 7). For most fish, the deviations from the group mean did not exceed one standard deviation. The number of such fish was especially high in experiments with indifferent for the minnow amino acids glutamine and proline, as well as in experiments with control pellets. The number of deviating fish can be expressed in percents of the group mean. As Table 8 shows, individual means of most fish did not differ from the group mean by more than 50%. The proportion of fish in which this difference exceeds 100% is small (for most kinds of pellets, 0–14% of all fish studied). However, for pellets with proline, the proportion of such fish is about 22%, and in experiments with phe-

**Table 6.** Values of the Spearman correlation coefficient between the consumption of pellets with L-alanine (0.1 M), L-glutamine (0.1 M), L-proline (0.1 M), L-phenylalanine (0.1 M), extract of Chironomidae larvae (175 g/l), and control pellets

| Stimulus | Glutamine | Proline | Phenylalanine | Control | Chironomidae extract |
|---|---|---|---|---|---|
| Alanine | 0.40** | 0.55*** | 0.30* | 0.50*** | 0.37* |
| Glutamine | | 0.48*** | 0.21 | 0.45** | 0.50*** |
| Proline | | | 0.44** | 0.53*** | 0.33* |
| Phenylalanine | | | | 0.49*** | 0.22 |
| Control | | | | | 0.30* |

Note: Significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

**Table 7.** The number of minnows differing by individual mean consumption of pellets from the group mean (measured in units of standard deviation)

| Stimulus | Number of individuals differing by individual mean consumption of pellets from the group mean | | | |
|---|---|---|---|---|
| | less than by 1σ | more than by 1σ | more than by 2σ | more than by 3σ |
| L-alanine (0.1 M) | 28 | 21 | 0 | 0 |
| L-glutamine (0.1 M) | 44 | 2 | 2 | 1 |
| L-proline (0.1 M) | 38 | 10 | 1 | 0 |
| Extract of Chironomidae larvae (175 g/l) | 25 | 23 | 1 | 0 |
| Control pellets | 41 | 6 | 1 | 1 |

**Table 8.** The number of minnows differing by individual mean consumption of pellets from the group mean (the value of the deviation in %)

| Stimulus | Number of individuals in which the individual mean: | | | | |
|---|---|---|---|---|---|
| | less than the group mean by | | 50% of the group mean | more than the group mean by | |
| | 100–150% | 50–100% | | 50–100% | 100–150% |
| L-alanine (0.1 M) | 0 | 15 | 21 | 9 | 4 |
| L-glutamine (0.1 M) | 0 | 25 | 15 | 4 | 1 |
| L-proline (0.1 M) | 0 | 19 | 16 | 3 | 11 |
| L-phenylalanine (0.1 M) | 38 | 0 | 0 | 0 | 11 |
| Extract of Chironomidae larvae (175 g/l) | 0 | 13 | 17 | 12 | 0 |
| Control pellets | 0 | 19 | 24 | 4 | 7 |

**Table 9.** The number of minnows differing by individual mean consumption of pellets from the group mean with different significance levels

| Stimulus | Number of individuals differing by individual mean consumption of pellets from the group mean with different significance levels | | | | | | |
|---|---|---|---|---|---|---|---|
| | heightened consumption | | | $p > 0.05$ | reduced consumption | | |
| | $p < 0.001$ | $p < 0.01$ | $p < 0.05$ | | $p < 0.05$ | $p < 0.01$ | $p < 0.001$ |
| L-alanine (0.1 M) | 4 | 4 | 4 | 28 | 3 | 6 | 0 |
| L-glutamine (0.1 M) | 3 | 0 | 3 | 43 | 0 | 0 | 0 |
| L-proline (0.1 M) | 6 | 0 | 1 | 42 | 0 | 0 | 0 |
| L-phenylalanine (0.1 M) | 1 | 0 | 0 | 48 | 0 | 0 | 0 |
| Extract of Chironomidae larvae (175 g/l) | 0 | 0 | 13 | 23 | 7 | 3 | 3 |
| Control pellets | 2 | 4 | 0 | 43 | 0 | 0 | 0 |

nylalanine, deviation of all individuals exceeds 100% because of low group mean consumption level. If the deviation is expressed by the number of individuals, with individual responses significantly different from the group mean, it is the highest for pellets with alanine and extract of Chironomidae larvae (Table 9).

## DISCUSSION

The minnow is a traditional object of experimental studies in ichthyology, including studies of behavior and sensory physiology. Many works on fish chemoreception, mainly olfactory, have been conducted on this species (Wrede, 1932; Frisch, 1938; Göz, 1941; Nweurath, 1949; Malyukina and Dmitrieva, 1967; Marusov, 1976; Malyukina *et al.*, 1977; Magurran, 1989; Essler and Kotrschal, 1994). The data on the taste of the minnow are limited to the topography and density of taste buds on the outer surface of the body (Gomahr *et al.*, 1992). The ability of minnows to develop conditioned reflexes to typical taste substances (quinine, sucrose, acetic acid) was determined without control experiments on chemosensory deprivation, and therefore the data obtained could actually be accounted for only by taste reception (Glaser, 1968). Recently, the temporal pattern of compensatory movements caused by prolonged anosmia and involving the taste system of fish was revealed in the minnow (Kasumyan and Marusov, 2002). The results of this study reflect the functional characteristics of the taste system of this fish species because earlier experiments have shown that removal of olfactory sensitivity does not alter the responses of the fish to pellets with taste substances (Kasumyan and Morsi, 1996).

Free amino acids are adequate stimuli and are often used in experimental studies of taste reception in fishes (Marui and Caprio, 1992). Taste properties of free amino acids differ, the preferences of fish to these substances are quite unique (Kasumyan, 1997). Among the four amino acids used, alanine had the stimulating effect to the minnows. The inclusion of this amino acid to the composition of artificial food pellets brought about an increased consumption also by many other cyprinid fishes (Cyprinidae)—carp, tench *Tinca tinca*, roach *Rutilus rutilus*, and fishes of other systematic groups: the starred sturgeon *Acipenser stallatus*, Siberian sturgeon *A. baeri* (Acipenseridae), and chum salmon *Oncorhynchus keta* (Salmonidae). In the goldfish *Carassius auratus*, trout *Salmo trutta*, arctic char *Salvelinus alpinus erythrinus*, lake char *S. namaycush* (Salmonidae), the Russian sturgeon *A. gueldenstaedtii* (Acipenseridae), and guppy *Poecilia reticulata* (Poeciliidae), alanine is an indifferent taste substance. The species differences are even more pronounced in responses of fish to glutamine, proline, and phenylalanine (Kasumyan and Sidorov, 1992, 1994, 2001; Kasumyan *et al.*, 1993; Kasumyan and Morsi, 1996; Kasumyan, 1999; Kasumyan and Prokopova, 2001; Kasumyan and Nikolaeva, 2002).

Pronounced individual variations in the expression of taste responses have been found in the minnow, as in the earlier studied carp (Kasumyan, 2000). Individual means of the consumption of the same food pellets, including control pellets, could significantly differ, and for certain stimuli (alanine, glutamine, extract of Chironomidae larvae) they include the whole range of possible responses, from 0 to 100%. However, the deviation from the group mean in most individual fish does not exceed ±1 SD. The number of fish which differ in the consumption of pellets by more than two standard deviations and more is only 3%. On the whole, in 11% of cases, individual mean consumption of pellets differs from the group mean by more than a factor of two, i.e., by 100%. The number of fish, the responses of which significantly differ ($p < 0.05$) from the group mean, is small for most kinds of pellets. But in experiments with alanine and extract of chironomids, the number of such fish is significantly higher and reaches almost a half of the number of tested individuals (Table 9). Using the example of alanine and chironomids larvae, it is clear that deviation of individual means from the group mean equally involves increase and decrease of the pellet consumption (Tables 8 and 9, Fig. 2). The same pattern has been noted in the carp. In minnows, as in the carp, individual variation depends on the taste attractiveness of the substance. The higher the attractiveness, the more stable are the responses and less expressed are individual differences (Fig. 1a).

There is a significant positive relationship between the consumption of pellets with different taste stimuli, which is most probably determined by similarities of the functional condition of the fish, in particular, their food motivation. It is known (Kasumyan, 1997) that satiation significantly affects the intensity of the expression of taste preferences by fish. Their feeding activity is also affected by many other environmental factors, influencing the physiological status (illumination, water temperature, the presence and turbulence of current, the density of food organisms, their availability and distribution, the structure of the environment, etc.). It changes in relation to various forms of life activity of the fish, such as spawning, migration, stress caused by alterations of the environmental conditions, social relations in the group, etc. (Nikolsky, 1974; Carter *et al.*, 1992; Kasumyan *et al.*, 1993; Winberg *et al.*, 1993; Mikheev *et al.*, 1997; Rowe and Dean, 1998; Wooton, 1998; Vogel and Beauchamp, 1999). In our study, some of these factors were controlled or their action was sorted out because various experiments were conducted with different pellets during the same limited time interval (2–3 h).

However, significant differences in the expression of taste preferences were found after detailed comparison of the consumption of the six kinds of pellets by the fish (minnows 3, 6, 7, 8, 9, 16, 28, 31, etc.). It is interesting that a significant deviation in the consumption of one kind of pellet in such individuals is not accompanied by similar deviations in the consumption of other

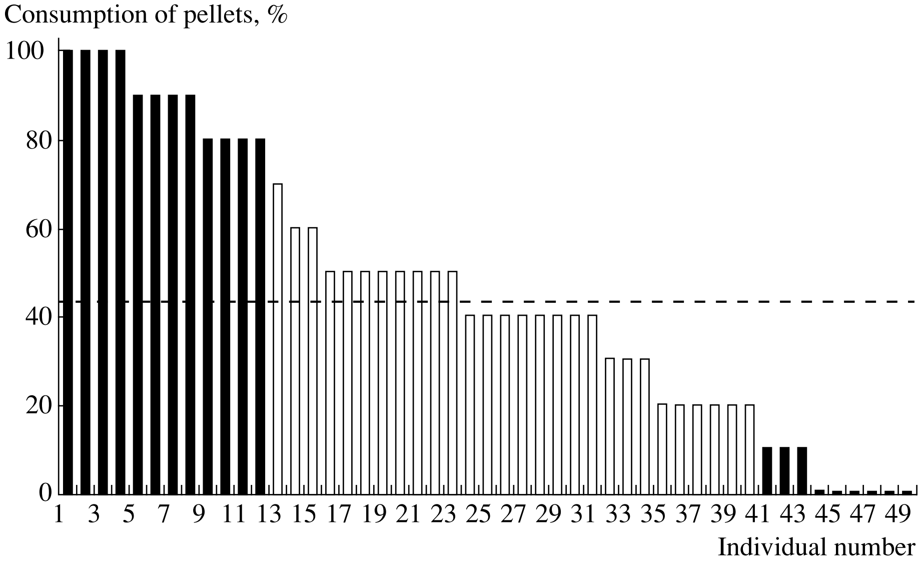

**Fig. 2.** Taste attractiveness of pellets with L-alanine (0.1M). Individuals significantly differing ($p < 0.02$, $\chi^2$ test) from the group mean consumption are given in black.

pellets. The specific response to the taste properties of many substances points to individual patterns of taste preferences in fish. Significant individual differences in taste preferences have been documented in humans: among 102 subjects, 16% were unable to discriminate the taste properties of sucrose (1.0%), 2% sodium chloride, 0.03% citric acid, and 0.01% caffeine. Two percent of subjects were characterized by increased sensitivity to all these stimuli. As in the minnows, in most subjects, the high sensitivity to one substance was not associated with high sensitivity to other substances (Golovnya *et al.,* 1980). Individual differences are expressed during comparison of the intensity of taste sensations caused in humans by different substances of the same quality (bitter), quinine sulfate, urea, and 6-n-propylthiouracil, suggesting possible individual differences in the expression of various pathways of transmission of taste stimuli (Yokomukai *et al.*, 1993).

Individual uniqueness of taste preferences in fish is probably genetically programmed. Several facts indirectly point to it: the absence of any clear differences in taste preferences in fish of the same species (the grass carp *Ctenopharyngodon idella*) raised on vegetal and animal food (Kasumyan and Morsi, 1997), in individuals from different populations (the trout of the Caspian, Baltic, and White seas) (Kasumyan and Sidorov, 1995), and in same-age conspecifics (yearlings of the carp) with the same origin but tested in different years (Kasumyan and Morsi, 1996; Kasumyan, 2000). The innate character of taste preferences was determined in mammals (Shinghai and Beidler, 1985; Lush, 1986), including humans (Hall *et al.*, 1975; Bartroshuk, 1979; Bertoshuk *et al.*, 1988). A gene involved in the ability of humans to identify the taste of certain substances has been found (Kalmus, 1971).

Unlike the consumption of pellets, the variations of other measures of the behavioral taste response, the retention time for the first snap and during the total experiment, were expressed weaker, but had the same relation to the taste attractiveness of pellets as their consumption (Fig. 1b). The most stable was the mean number of snaps. In most fish, for all kinds of pellets, it ranged from 1.0 to 1.1 and only in very rare cases exceeded 1.5. The minnow is a rheophilous species inhabiting streams and small rivers. It usually keeps on riffles and feeds mainly on drift (Nikolsky *et al.*, 1947; Bazikalova and Valisova, 1959; Tugarina *et al.*, 1965). Under such conditions, frequent rejections and repeated bites could cause the loss of the prey item. This pattern of feeding behavior is characteristic not only of the minnow but also other river species as well as of fish living in the tidal zone of the marine shore (Kasumyan and Sidorov, 1994; Kasumyan and Nikolaeva, 2002). The relatively short testing of the pellet, never exceeding 5 s even for attractive alanine and chironomid extract, is also characteristic of the minnow. Bentivorous fish retain the pellet longer; for example, the tench retains highly attractive pellets with citric acid for 26 s, and carp retain pellets with cysteine about 17 s (Kasumyan and Morsi, 1996; Kasumyan and Prokopova, 2001).

Even though the retention time is short in the minnow, this species is characterized by a positive relationship between this measure of the behavioral taste response and the level of pellet consumption. This relation is expressed in all kinds of pellets, excluding only pellets with chironomid extract (Table 10). Earlier, the same pattern of responding was documented in the carp, trout, tench, and guppy (Kasumyan and Sidorov, 1994; Kasumyan and Morsi, 1996; Kasumyan and Nikolaeva, 1997; Kasumyan and Prokopova, 2001),

**Table 10.** Spearman correlation coefficients between measures of the behavioral taste response of minnows to pellets with (1) L-alanine (0.1 M), (2) L-glutamine (0.1 M), (3) L-proline (0.1 M), (4) L-phenylalanine (0.1 M), (5) extract of Chironomidae larvae (175 g/l), and (6) control pellets

| Measure | Number of snaps | | | | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Pellets consumption, % | –0.18 | 0.22 | 0.56*** | 0.26 | –0.40** | 0.18 |
| Number of snaps | | | | | | |
| Retention time after the first snap | | | | | | |

| Measure | Retention time | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | after the first snap | | | | | | during the whole experiment | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 |
| Pellets consumption, % | 0.84*** | 0.83*** | 0.84*** | 0.50*** | 0.19 | 0.85*** | 0.79*** | 0.88*** | 0.82*** | 0.55*** | 0.05 | 0.86*** |
| Number of snaps | –0.30* | 0.11 | 0.54*** | 0.24 | 0.12 | 0.06 | 0.04 | 0.34* | 0.75*** | 0.42** | 0.44** | 0.34* |
| Retention time after the first snap | | | | | | | 0.91*** | 0.95*** | 0.93*** | 0.94*** | 0.89*** | 0.93*** |

Note: See Note to Table 6.

suggesting that this may be common to all fishes. The statistically significant relationship between the number of snaps for most kinds of pellets was documented only with respect to the duration of retention of the pellet during the total experiment, but the value of the correlation coefficient is rather small. In other fish species, excluding tench, there is no relation between the number of snaps and other measures of the behavioral taste response.

Individual variation is a characteristic trait of fish behavior, including social, defensive, reproductive, etc. (Murphy and Pitcher, 1991; Magurran, 1993; Diana, 1995). Individual differences in feeding behavior usually involve different levels of feeding activity of individuals within the group (Brännäs and Alänära, 1993), the duration and speed of swimming during the food search, variation in the distance of hunting drop to the prey (McLaughlin *et al.*, 1992; Biro and Ridgway, 1995), the use of various strategies of feeding behavior (Ringler, 1983; Ehlinger, 1989, 1990; McLaughlin *et al.*, 1992, 1999), and different intensity of feeding and, as a consequence, different growth rate (Davis and Olla, 1987; McCarthy *et al.*, 1992; Jobling and Koskela, 1996; Salvanes and Hart, 1998). One cause of within-group or within-population variations may be associated with differences in their taste preferences.

This characteristic of the taste reception of fish is very important for the understanding of the mechanisms bringing about the use of various food organisms by individuals of the same species, living within the same habitat or maintained under the same conditions (Allen, 1941; Bryan and Larkin, 1972; Smagula and Adelman, 1982; Ringler, 1985; Bridcut and Giller, 1995; Amundsen *et al.*, 1995) or differences between fish in the consumption of the same food (Salvanes and Hart, 1998). It is possible that different taste preferences or different degrees of their expression could lead to the divergence of fish with respect to the consumed food objects and feeding behavior, and bring about food specialization, exploitation of different niches within the habitat, and the development of morphs, forms, ecotypes, and other intrapopulation groups. Such differences are well pronounced in polymorphic species, for example, in arctic chars of the genus *Salvelinus* or in the trout (Savvaitova, 1989; Ferguson, 1989; Malmquist, 1992) and other fishes. Feeding specialization reduces within-group competition and causes more complete use of the food resource of the water body (Meyer, 1990; Holbrook and Schmitt, 1992).

These data could be used in aquaculture to reduce the heterogeneity of the consumption of artificial food and the differentiation of fish with respect to the growth rate (Yamagishi *et al.*, 1974; Storebakken and Austereng, 1988; Hustvedt *et al.*, 1991; McCarthy *et al.*, 1992, 1993). A perspective way to solve this important applied problem may be creation of new breeds of fish, which have reduced requirements to the qualities of artificial foods. It could be possible, by selection of individuals with certain taste patterns, to breed with subsequent directed selection of the offspring. The knowledge of the range of individual differences of fish by taste preferences are necessary for the development of highly efficient chemical stimulators, additions to artificial foods, and development of artificial lures and fishing gear (both commercial and sport).

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## REFERENCES

Allen, K.R., Studies on the Biology of the Early Stages of the Salmon (*Salmo salar*). II. Feeding Habits, *J. Anim. Ecol.*, 1941, vol. 10, pp. 47–76.

Amundsen, P.-A., Damsgård, B., Arnsen, A.M., Jobling, M., and Jørgensen, E.H., Experimental Evidence of Cannibalism and Prey Specialization in Arctic Char, *Salvelinus alpinus*, *Environ. Biol. Fish.*, 1995, vol. 43, pp. 285–293.

Bartochuk, L.M., Rifkin, B., Marks, L.E., and Hooper, J.E., Bitterness of KCl and Benzoate: Related to Genetic Status for Sensitivity to PTC/PROP, *Chemical Senses*, 1988, vol. 13, pp. 517–528.

Bartoshuk, L.M., Bitter Taste of Saccharin Related to the Genetic Ability to Taste the Bitter Substance 6-n-propylthiouracil, *Science*, 1979, vol. 205, pp. 934–935.

Bazikalova, A.Ya. and Vilisova, I.K., Feeding of Bentivorous Fish of the Smaller Sea, *Tr. Baikalskoi Limnol. St., Akad. Nauk SSSR*, 1959, vol. 17, pp. 382–497.

Beaudoin, C.P., Tonn, W.M., Prepas, E.E., and Wassenaar, L.I., Individual Specialization and Trophic Adaptability of Northern Pike (*Esox lucius*): An Isotope and Dietary Analysis, *Oecologia*, 1999, vol. 120, pp. 386–396.

Biro, P.A., Ridgway, M.S., Individual Variation in Foraging Movements in a Lake Population of Young-of-the-Year Brook Charr (*Salvelinus fontinalis*), *Behaviour*, 1995, vol. 132, pp. 57–74.

Brannas, E. and Alanara, A., Monitoring the Feeding Activity of Individual Fish with a Demand Feeding System, *J. Fish Biol.*, 1993, vol. 42, pp. 209–215.

Bridcut, E.E. and Giller, P.S., Diet Variability and Foraging Strategies in Brown Trout (*Salmo trutta*): An Analysis from Subpopulations to Individuals, *Can. J. Fish. Aquat. Sci.*, 1995, vol. 52, pp. 2543–2552.

Bryan, J.E. and Larkin, P.A., Food Specialization by Individual Trout, *J. Fish. Res. Bd. Canada*, 1972, vol. 29, pp. 1615–1624.

Carter, C.G., Huolihan, D.F., McCarthy, I.D., and Bratield, A.E., Variation in the Food Intake of Grass Carp, *Ctenopharyngodon idella* (Val.), fed Singly or in Groups, *Aquat. Living Resour.*, 1992, vol. 5, pp. 225–228.

Davis, M.W. and Olla, B.L., Aggression and Variation in Growth of Chum Salmon (*Oncorhynchus keta*) Juveniles in Seawater: Effects of Limited Rations, *Can. J. Fish. Aquat. Sci.*, 1987, vol. 44, pp. 192–197.

Diana, J.S., Social Behaviour, in *Biology and Ecology of Fishes*, Carmel: Cooper, 1995, pp. 253–280.

Ehlinger, T.J., Habitat Choice and Phenotype-Limited Feeding Efficiency in Bluegill: Individual Differences and Trophic Polymorphism, *Ecology*, 1990, vol. 71, pp. 886–896.

Ehlinger, T.J., Learning and Individual Variation in Bluegill Foraging: Habitat-Specific Techniques, *Anim. Behav.*, 1989, vol. 38, pp. 643–658.

Essler, H. and Kotrschal, K., High Resolution Analysis of Swim Path Patterns of Intact and Olfaction-Deprived Minnows (*Phoxinus phoxinus*) Stimulated with Food and Potential Predator Odour, *J. Fish Biol.*, 1994, vol. 45, pp. 555–567.

Ferguson, A., Genetic Differences among Brown Trout *Salmo trutta* Sticks and their Importance for Conservation and Management of the Species, *Freshwat. Biol.*, 1989., vol. 21, pp. 35–46.

Frisch, K., von, Uber einen Schreckstoffder Fischhaut und seine biologische Bedeutung, *Z. vergl. Physiol.*, 1941, vol. 29, no. 1. pp. 46–145.

Frisch, K., von, Zur Psychologie des Fischwannes, *Naturwissenschaften*, 1938, vol. 26, pp. 601–606.

Glaser, D., Zum Verhalten blinder Fische, *Z. Tierpsychol.*, 1968, vol. 25, no. 6, pp. 648–658.

Golovnya, R.V., Yakovleva, V.N., Chesnokova, A.E., Borisov, Yu.A., and Matveeva, A.V., Individual Differences of Taste Sensitivity in Humans based on Choice of Tasters, in *Sensorniye sistemy. Obonyaniye i vkus* (Sensory Systems. Olfaction and Taste), Leningrad: Nauka, 1980, pp. 148–158.

Gomahr, A., Palzenberger, M., and Kotrschal, K., Density and Distribution of External Taste Buds in Cyprinids, *Environ. Biol. Fish.*, 1992, vol. 33, no. l–2, pp. 125–134.

Goz, H., Uber den Arts und Individualgeruch bei Fischen, *Z. vergl. Physiol.*, 1941, vol. 29, pp. 1–45.

Gu, B., Schelske, C.L., Hoyer, M.V., Intrapopulation Feeding Diversity in Blue Tilapia: Evidence from Stable-Isotope Analysis, *Ecology*, 1997, vol. 78, pp. 2263–2266.

Hall, M.J., Bartoshuk, L.M., and Cain, W.S., PTC Taste Blindness and the Taste of Caffeine, *Nature*, 1975, vol. 235, pp. 851–853.

Haugen, T.O., Rygg, T.A., Foods and Habitat Segregation in Sympatric Grayling and Brown Trout, *J. Fish Biol.*, 1996, vol. 49, no. 2, pp. 301–318.

Holbrook, S.J. and Schmitt, R.J., Causes and Consequences of Dietary Specialization in Surf Perches: Patch Choice and Intraspecific Competition, *Ecology*, 1992, vol. 73, pp. 402–412.

Hustvedt, S.V., Storebakken, T., and Salte, R., Does Oral Administration of Oxolinic Acid or Oxytetracycline Affect Feed Intake of Rainbow Trout? *Aquaculture*, 1991, vol. 92, pp. 109–113.

Jobling, M. and Koskela, J., Interindividual Variations in Feeding and Growth in Rainbow Trout during Restricted Feeding and in a Subsequent Period of Compensatory Growth, *J. Fish Biol.*, 1996, vol. 49, pp. 658–667.

Kalmus, H., The Genetics of Taste, in *Hanbook of Sensory Physiology, vol. 4. Chemical Senses, pt. 2: Taste*, Beidler, L.M., Ed., New York: Springer 1971, pp. 165–179.

Kasumyan, A.O., Individual Variability of Taste Preferences and the Behavior taste Response to Taste Stimuli in the Carp, *Cyprinus carpio*, *Vopr. Ikhtiol.*, 2000, vol. 40, no. 5, pp. 693–702.

Kasumyan, A.O., Olfaction and Taste Senses in Sturgeon Behaviour, *J. Appl. Ichthyol.*, 1999, vol. 15, pp. 228–232.

Kasumyan, A.O., Sidorov, S.S. and Pashchenko, N.I., The Effect of Water Temperature on Taste Sensitivity in Juvenile

Starred Sturgeon *Acipenser stellatus* to Free Amino Acids, *Dokl. Ross. Akad. Nauk*, 1993, vol. 331, no. 2, pp 248–250.

Kasumyan, A.O., Taste Reception and Feeding Behavior in Fishes, *Vopr. Ikhtiol.*, 1997, vol. 37, no. 1, pp. 78–93.

Kasumyan, A.O. and Marusov, E.A., behavioral Responses of the Minnow *Phoxinus phoxinus* (Cyprinidae) to Chemical Signals in Norm and after Acute and Chronic Anosmia, *Vopr. Ikhtiol.*, 2002, vol. 42, no. 4.

Kasumyan, A.O. and Morsi, A.M.Kh., Taste Preferences of Classical Taste Substances by Juvenile Grass carp *Ctenopharyngodon idella* (Cyprinidae, Pisces), Raised on Animal and Vegetate Foods, *Dokl. Ross. Akad. Nauk.*, 1997, vol. 357, no. 2, pp. 284–286.

Kasumyan, A.O. and Morsi, A.M.Kh., Taste Sensitivity of the Carp *Cyprinus carpio* to Free Amino Acids and Classical Taste Substances, *Vopr. Ikhtiol.*, 1996, vol. 36, no. 3, pp. 386–399.

Kasumyan, A.O. and Nikolaeva, E.V., A Comparative Study of Taste Preferences in Fish with Different Ecology and Feeding, *Vopr. Ikhtiol.*, 2002, Suppl. 2.

Kasumyan, A.O. and Nikolaeva, E.V., Taste Preferences of the Guppy *Poecilia reticulata* (Cyprinodontiformes), *Vopr. Ikhtiol.*, 1997, vol. 37, no. 5, pp. 696–703.

Kasumyan, A.O. and Prokopova, O.M., Taste Preferences and the Dynamics of Behavioral Taste Response in the Tench *Tinca tinca* (Cyprinidae), *Vopr. Ikhtiol.*, 2001, vol. 41, no. 5, pp. 670–685.

Kasumyan, A.O. and Sidorov, S.S., Comparative Analysis of Taste Responses of Juvenile Trout *Salmo trutta* in Populations of the Baltic and White Seas, *Dokl. Ross. Akad. Nauk*, 1995, vol. 343, no. 3, pp. 417–419.

Kasumyan, A.O. and Sidorov, S.S., Taste Properties of Free Amino Acids for Juvenile Caspian Trout *Salmo trutta caspicus* Kessler, *Vopr. Ikhtiol.*, 1994, vol. 34, no. 6, pp. 831–838.

Kasumyan, A.O. and Sidorov, S.S., Taste Sensitivity of the Chum Salmon *Oncorhynchus keta* to Basic Types of Taste Stimuli and Amino Acids, *Sens. Sist.*, 1992, vol. 6, no. 3, pp. 100–103.

Kasumyan, A.O. and Sidorov, S.S., Taste Sensitivity of the Lake Char *S. namaycush* (Salmonidae), *Vopr. Rybolovstva*, 2001, Suppl. 1, pp. 121–125.

Lush, I.E., The Genetics of Tasting in Mice, *Genet. Res.*, 1986, vol. 47, pp. 117–123.

Magurran, A.E., Acquired Recognition of Predator Odour in the European Minnow (*Phoxinus phoxinus*), *Ethology*, 1989, vol. 82, pp. 216–223.

Magurran, A.E., Individual Differences and Alternative Behaviours, in *Behaviour of Teleost Fishes*, Pitcher, T.J., Ed., London: Chapman and Hall, 1993, pp. 441–477.

Malmquist H.J., Phenotype-specific Feeding Behaviour of two Arctic Charr *Salvelinus alpinus morphs, Oecologia*, 1992, vol. 92, pp. 354–361.

Malyukina, G.A, Kasumyan, A.O., Marusov, E.A., and Pashchenko, N.I., The Alarm Substance and Its Significance in Fish Behavior, *Zh. Obshch. Biol.*, 1977, vol. 38, no. 1, pp. 123–131.

Malyukina, G.A. And Dmitrieva, N.G., A Study of the Characteristics of the Cemical Sense in the Minnow in relation to Schooling Behavior of Fish, *Vopr. Ikhtiol.*, 1967, vol.7, no. 1, pp. 156–167.

Marm, T., Caprio, J., Teleost Gustation, *Fish Chemoreception*, Hara, T.J., Ed., London: Chapman and Hall, 1992, pp. 171–198.

Martell, D.J., McClelland, G., Diets of Sympatric Flatfishes, *Hippoglossoides platessoides*, *Pleuronectes ferrugineus*, *Pleuronectes americanus* from Sable Island Bank, Canada, *J. Fish Biol.*, 1994, vol. 44, pp. 821–848.

Marusov, E.A. Ecological Stereotypes of Defensive Behavior of Fish to Chemical Signals of Danger, *Dokl. Vyshch. Shk. Biol. Nauki*, 1976, no. 8, pp. 67–69.

McCarthy, I.D., Carter, C.G., and Houlihan, D.F., The Effect of Feeding Hierarchy on Individual Variability in Daily Feeding of Rainbow Trout, *Oncorhynchus mykiss* (Walbaum), *J. Fish Biol.*, 1992, vol. 41, pp. 257–263.

McCarthy, I.D., Houlihan, D.F., Carter, C.G., and Moutou, K. Variation in Individual Food Consumption Rates of Fish and Its Implications for the Study of Fish Nutrition and Physiology, *Proc. Nutrition Soc.*, 1993, vol. 52, pp. 427–436.

McLaughlin, R.L., Ferguson, M.M., and Noakes, D.L.G., Adaptive Peaks and Alternative Foraging Tactics in Brook Charr: Evidence of Short-Term Divergent Selection for Sitting-and-Waiting and Actively Searching, *Behav. Ecol. Sociobiol.*, 1999, vol. 45, pp. 386–395

McLaughlin, R.L., Grant, J.W.A., and Kramer, D.L., Individual Variation and Alternative Patterns of Foraging Movements in Recently-Emerged Brook Charr (*Salvelinus fontinalis*), *Behaviour*, 1992, vol. 120, pp. 286–301.

Meyer, A., Ecological and Evolutionary Consequences of the Trophic Polymorphism in *Cichlasoma citrinellum* (Pisces: Cichlidae), *Biol. J. Linnean Soc.*, 1990, vol. 39, pp. 279–299.

Mikheev, V.N., Afonina, M.O., and Gaisina, E.V., Visually Heterogeneous Environment Stimulates the Feeding Activity in Cichlid Fish, *Vopr. Ikhtiol.*, 1997, vol. 37, no. 1, pp. 101–105.

Murphy, K.E. and Pitcher, T.J., Individual Behavioural Strategies Associated with Predator Inspection in Minnow Shoals, *Ethology*, 1991, vol. 88, pp. 307–319.

Neurath, H., Uber die Leistung des Geruchssinnes bei Ehitzen, *Z. vergl. Physiol.*, 1949, vol. 31, pp. 609–626.

Nikolsky, G.V., *Ekologiya ryb* (Fish Ecology), Moscow: Vysshaya Shkola, 1974.

Nikolsky, G.V., Gromchevskaya, N.A., Morozova, G.I., and Pikuleva, V.A., *Rybi basseina Verkhnei Pechory* (Fishes of the Basin of Verkhnyaya Pechora), Moscow: Mosk. Obshch. Ispyt. Prirody, 1947.

Ringler, N.H., Individual and Temporal Variation in Prey Switching by Brown Trout *Salmo trutta*, *Copeia*, 1985, no. 4, pp. 918–926.

Ringler, N.H., Variation in Foraging Tactics of Fishes, in *Predators and Prey in Fishes*, Noakes, D.L.G., Linquist, D.G., Helfman, G.S. and Ward, J.A., Eds., The Hague: Junk, 1983, pp. 159–172.

Rowe D.K., Dean T.L., Effects of Turbidity on the Feeding Ability of the Juvenile Migrant Stage of Six New Zealand Freshwater Fish Species, *New Zealand J. Mar. Freshwater Res.*, 1998, vol. 32, pp. 21–29.

Salvanes, A.G.V. and Hart, P.J.B., Individual Variability in State-Dependent Feeding Behaviour in Three-Spined Sticklebacks, *Anim. Behav.*, 1998, vol. 55, pp. 1349–1359.

Samo, B., Glass, C.W., and Smith, G.W., Differences in Diet and Behaviour of Sympatric Saithe and Pollack in a Scottish Sea Loch, *J. Fish Biol.*, 1994, vol. 45, Suppl. A, pp. 1–11.

Savvaitova, K.A., *Arkticheskiye goltsy* (Arctic Chars), Moscow: Agropromizdat, 1989.

Schindler, D.E., Hodgson, J.R., and Kitchell, J.F., Density-Dependent Changes in Individual Foraging Specialization of Largemouth Bass, *Oecologia*, 1997, vol. 110, pp. 592–600.

Shingai, T. and Beidler, L.M., Inter-Strain Differences in Bitter Taste Responses in Mice, *Chemical Senses*, 1985, vol. 10, pp. 51–55.

Smagula, C.M. and Adelman, I.R., Day-to Day Variation in Food Consumption by Largemouth Bass, *Trans. Amer. Fish. Soc.*, 1982, vol. 111, pp. 543–548.

Storebakken, T. and Austreng, E., Feed Intake Measurements in Fish Using Radioactive Isotopes. II. Experiments with Atlantic Salmon and Rainbow Trout in Sea-Pens, *Aquaculture*, 1988, vol. 70, pp. 277–288.

Svardson, G., Interspecific Population Dominance in Fish Communities of Scandinavian Lakes, *Rep. Hist. Freshwater Res. Drottningholm*, 1976, vol. 55, pp. 144–171.

Tugarina, P.Ya, Antipova, N.L., and Rostovtseva, L.A., On Feeding of the Minnow *Phoxinus phoxinus* in the Basin of Bailkal and Irkutsk Reservoir, *Izv. Biol.–Geogr. Nauchno-Issled. Inst. pri Irkutsk Gos. Univ.*, 1965, vol. 18, nos. 1–2, pp. 108–134.

Vander Zanden, M.J., Shuter, B.J., Lester, N.P., and Rasmussen, J.B., Within- and Among-Population Variation in the Trophic Position of a Pelagic Predator, Lake Trout (*Salvelinus namaycush*), *Can. J. Fish. Aquat. Sci.*, 2000, vol. 57, pp. 725–731.

Vogel, J.L. and Beauchamp, D.A., Effects of Light, Prey Size, and Turbidity on Reaction Distances of Lake Trout (*Salvelinus namaycush*) to Salmonid Prey, *Can. J. Fish Aquat. Sci.*, 1999, vol. 56, pp. 1293–1297.

Winberg, S., Carter, C.G., McCarthy, I.D, He, Z.-Y., Nilsson, G.E., and Houlihan, D.F., Feeding Rank and Brain Serotonergic Activity in Rainbow Trout *Oncorhynchus mykiss*, *J. exp. Biol.*, 1993, vol. 179, pp. 197–211.

Wootton, R.J., *Ecology of Teleost Fishes*, Dordrecht: Kluwer, 1998.

Wrede, W.L., Versuche ber den Artduft der Eiritzen, *Z. vergl. Physiol.*, 1932, vol. 17, no. 3, pp. 510–519.

Yamagishi, H., Maruyama, T., and Mashiko, K., Social Relation in Small Experimental Population of *Odontobitus obscurus* (Temminck et Schlegel) as Related to Individual Growth and Food Intake, *Oecologia*, 1974, vol. 17, pp. 187–202.

Yokomukai, Y., Cowart, B.J., and Beauchamp, O.K., Individual Differences in Sensitivity to Bitter-Tasting Substances, *Chemical Senses*, 1993, vol. 18, no. 6, pp. 669–681.

Zerba, K.E. and Collins, J.P., Spatial Heterogeneity and Individual Variation in Diet of an Aquatic Top Predator, *Ecology*, 1992, vol. 73, pp. 268–279.

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