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Influence of Age and Size on the Response to Novel Prey by Fry of the Cichlid Fish *Cichlasoma managuense* (Pisces: Cichlidae)

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With 2 figures

Abstract

The response to a novel prey item was investigated during the first month of feeding of the cichlid fish *Cichlasoma managuense*. The relative contribution of size and age to improvement in predatory behavior was addressed. Group I (control) was fed nauplii of *Artemia salina* and group II a manufactured flakefood diet. Group II fish were tested for their ability to prey on a novel diet, the nauplii of *Artemia salina*. Latency to respond to the presence of novel prey decreased and the number of capture attempts increased with increasing experience with the artificial diet and with age. As size increased so did the number of capture attempts, but the latency did not change. Size and experiential and maturational factors may affect parts of the predatory behavior differentially. During the first month of feeding, age may be more important than size for the decrease in latency and the increase in the number of capture attempts. The number of capture attempts during the first 30 s of the observation period and the capture success increased faster than the latency decreased. Latency to respond to novel prey may mature at a slower rate than the number of capture attempts.

Introduction

Particularly during ecological bottlenecks natural selection should favor animals that can prey on a variety of diets (SCHOENER 1971; CURIO 1976; WIENS 1977). The ability to exploit new food sources efficiently depends on the ability of the animal to recognize, catch, and handle various types of prey. Yet, novelty of the prey's behavior, color, size, and taste may deter predators unfamiliar with this novel diet (BURGHARDT 1966, 1967, 1969; BURGHARDT & HESS 1966; SUTTERLIN & SUTTERLIN 1970; WARE 1971, 1972; SHETTLEWORTH 1972; BRYAN 1973; RINGLER 1979; MEYER 1986, 1987; but see refs. in CURIO 1976; OHGUCHI 1978).

In fishes, mortality due to starvation and predation is particularly high in young age classes (e.g., HUNTER 1981). Fish larvae cannot search a large volume of water, prey is often patchily distributed, and the composition of the zooplankton is variable (ROSENTHAL 1969; BOHL 1982). This seems to hold also even for cichlid fish in which predation pressure on fry is high despite parental protection (McKAYE & BARLOW 1976).

Fish larvae encounter a variety of potential prey types. Ontogenetic dietary changes in cichlid young have been reported (DE MOOR et al. 1986). Young fish that quickly recognize and respond to a diversity of prey probably grow faster and have a better chance of escaping the high mortality rates of early life history stages. However, an alternative scenario is possible: early specialization may in a constant environment, with a stable supply of prey, lead to faster growth. This idea is supported by ROSENTHAL (1969) who reported that individual herring larvae, even after a few feeding experiences with a novel prey, did not attempt to catch novel prey at the same rate as familiar prey. He suggested that individual fry became trained to respond preferentially to particular prey that they have captured with high success. BURGHARDT's pioneer studies (e.g. 1966, 1967, 1969) on prey selection in young reptiles have addressed these questions in an exemplary manner.

Feeding success is often correlated with the morphology and size of the larvae (HUNTER 1972, 1981; BROWN & COLGAN 1984, 1985; BLAXTER 1986; COLGAN et al. 1986; MEYER 1987). This has also been reported for parts of the predatory behavior of salamander larvae (LEFF & BACHMANN 1986). However, behavioral changes during ontogeny can occur without morphological correlates: MEYER (1986) found in 10-day old fry of Cichlasoma managuense that one or two feeding experiences with a novel prey significantly increased the fry's ability to capture a novel type of prey and to discriminate it from unpalatable prey. Also juvenile garter snakes change their behavior towards different prey with increasing age and experience without correlated changes in morphology (e.g. FUCHS & BURGHARDT 1971).

The responsiveness of fish fry to novel prey stimuli is influenced by the correlated factors of age and size. This study asks which behavioral component of predation on novel prey is more strongly influenced by age or size.

Materials and Methods

The fry of the piscivorous Central American cichlid fish Cichlasoma managuense used in this experiment were from one spawning. They were separated from the parents after hatching, but before free-swimming and the onset of exogenous feeding. I randomly assigned them to group I (control) or group II (treatment) with about 300 fish in each group. Each group was kept in a 60-l tank with 12 : 12 h light : dark at 27 ± 1 °C. The fry were fed twice daily ad libitum. Group I fry were fed nauplii of Artemia salina. Group II fry were fed pulverized flakefood (Kordon Products).

Almost every day, for the first month of feeding, I tested two fish of each group for their ability to prey on nauplii. For group II fish this represented a switch from flakefood to the novel prey, nauplii of Artemia salina. The reciprocal switch from nauplii to flakefood was not conducted because fry only reluctantly fed on flakefood when presented as novel prey and responded much more rapidly to moving and natural looking prey. This has also been observed in young white sturgeons (LINDBERG & DOROSHOV 1986).

The novel prey used in this study, nauplii of *Artemia salina*, are easy for the fish to catch. The first-feeding efficiency of *C. managuense* is about 70% (MEYER 1987) and improves to almost 100% in less than 10 days after the onset of feeding (MEYER, unpubl. data). Therefore when group II was switched to nauplii of *Artemia salina* the fry were probably not deterred from switching by evasive prey.

Fry were chosen randomly from holding tanks and placed singly into separate observation tanks (10 × 10 × 10 cm). The fry were acclimated for 3 h, together with one other fry from the same group serving as dither (BARLOW 1968) to increase calmness of the fish. During the 5-min observation period the behavior of only one, predetermined fry was recorded using focal-animal sampling (ALTMANN 1974).

Approximately 500 *Artemia salina* nauplii were introduced into the observation tanks. Latency, the time between the introduction of the prey and the first capture attempt of the fish, was recorded (in s). During the 5-min observation all capture attempts were counted within 10 successive 30-s time intervals. Latency, number of attempts made in the first 30 s of observation, and total number of attempts are reported here. Capture success, the number of prey caught in an observation period, and the number of attempts are closely correlated in *C. managuense* (MEYER 1987).

After observation, tested fry and dither fish were anaesthetized with phenoxyethanol, sacrificed, and fixed in 10% buffered formalin. Hence each fry was tested only once, ensuring statistical independence of the data.

Later the fry were measured (total length) and weighed (wet weight included the weight of the captured prey). Some of the vials in which fry were stored dried out before this part of the study was completed. This reduced the sample size for some statistical tests. Data were log-transformed for the statistical tests which were performed using the SYSTAT statistical package (WILKINSON 1986).

Results

Fry improved their predation success during the first 30 days (Fig. 1). All regression slopes (Figs. 1, 2), except latency regressed on size in group II (Fig. 2A), were significantly different from 0 at the 0.05 level (regression analysis, regression equations in legends of figures). Comparisons by simple t-tests showed that the two groups were significantly different in all variables.

Behavioral Changes and Age

Latency: Fish of both groups had similar latencies at the beginning of feeding on nauplii (Fig. 1A). The latency of the control group (I) decreased at a significantly faster rate with increasing age ($F = 4.95$, $p = 0.028$; Fig. 1A). After about a week of feeding on nauplii the latency of the control group fluctuated between 1 and 2 s. Even without prior experience with nauplii, group II's latency decreased significantly with age (regression analysis: $F = 6.142$, $df = 46$, $p < 0.05$). Group II's latency fluctuated around 10 s after 10 to 15 days. Overall means between the groups were significantly different with group I having a shorter latency (ANOVA: $t = 5.58$, $df = 98$, $p < 0.000$; Gr I: $\overline{X} = 2.96$, $SD = 2.60$; Gr II: $\overline{X} = 7.62$, $SD = 5.36$).

Attempts in first 30 s: Fish of both groups increased the number of capture attempts made during the first 30 s with age (Fig. 1B). Both groups showed the same rate of behavioral change as confirmed by homogeneity of their slopes ($F = 2.4$, $p = 0.124$; Fig. 1B). However, the number of attempts in the first 30 s was significantly higher for fry with prior experience with nauplii (ANOVA: $t = 5.28$, $df = 97$, $p < 0.000$; Gr I: $\overline{X} = 30.0$, $SD = 13.44$; Gr II: $\overline{X} = 17.5$, $SD = $
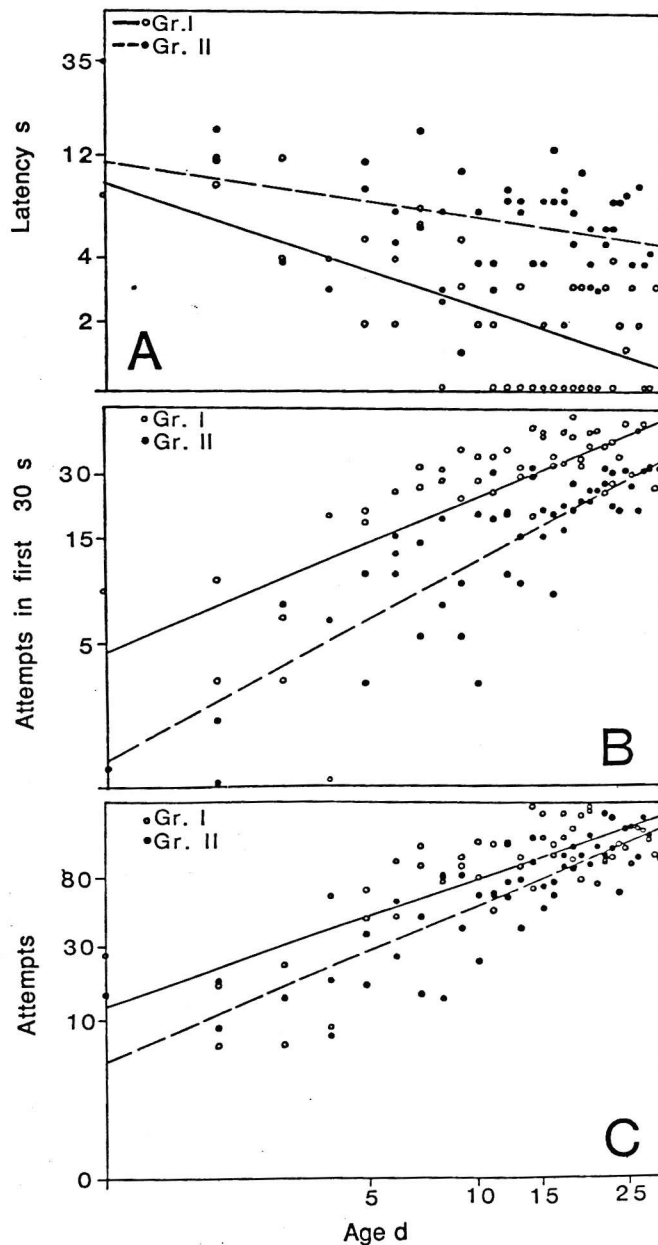
Fig. 1: A: Change in latency to respond to the presence of the novel prey. Group I (control) had previous feeding experience with the novel prey. Group II had no previous feeding experience with the novel prey, the nauplii of *Artemia salina*. The regression equations in this and the following figures are significant at least at the 0.05 level (if not stated otherwise in the text). The regression equations were calculated from log-transformed data. Regression equations: Group I, latency $= 1.013 + -0.6413 \times$ age, $r^2 = 0.4712$. Group II, latency $= 1.115 + -0.2774 \times$ age, $r^2 = 0.1618$.

B: Change in the number of capture attempts made during the first 30 s of the observation period with increasing age. Regression equations: Group I, attempts in first 30 s $= 0.5914 + 0.7665 \times$ age, $r^2 = 0.5616$. Group II, attempts in first 30 s $= 0.0846 + 0.9898 \times$ age, $r^2 = 0.7265$. C: Change in the number of capture attempts during the whole observation period with increasing age. Regression equations: Group I, attempts $= 1.07697 + 0.825313 \times$ age, $r^2 = 0.6079$. Group II, attempts $= 0.7416 + 1.007 \times$ age, $r^2 = 0.7395$

9.35). The difference between the groups became smaller as the fish aged (Fig. 1B), i.e. the slopes tended to converge.

Attempts: Fish of both groups showed a comparable rate of change in the number of attempts made during the whole observation period. The total number of attempts was significantly higher in group I (ANOVA: t = 2.6, df = 98, p <

0.05; Gr I: $\overline{X}$ = 113.1, SD = 59.16; Gr II: $\overline{X}$ = 83.1, SD = 56.01). The trend was similar to the trend in the attempts in the first 30 s (Fig. 1C); with age the number of attempts made became more similar. The lines converged, but not significantly (F = 1.95, p = 0.166).

Weight: The fish in group II weighed (g) less than the fish in the control group (ANOVA: F = 9.22, df = 86, p < 0.005; Gr I: $\overline{X}$ = 0.24, SD = 0.021; Gr II: $\overline{X}$ = 0.13, SD = 0.011). The rates of weight increase with age were not significantly different (F = 1.36, p = 0.247) between the groups. The regression equations for log-transformed data are: (group I) weight = −2.9 + 1.0873 × age, r = 0.86; (group II) weight = −3.03 + 0.9659 × age, r = 0.79.

Total length: The fish in group II increased in length (mm) at the same rate (F = 1.1, p = 0.298) but were smaller than fish in the control group (ANOVA: F = 7.13, df = 68, p < 0.01; Gr I: $\overline{X}$ = 11.3, SD = 3.25; Gr II: $\overline{X}$ = 9.45, SD = 2.49). The regression equations for log-transformed data are: (group I) total length = 0.665 + 0.344 × age, r = 0.83; (group II) total length = 0.638 + 0.303 × age, r = 0.77.

Behavioral Changes and Size

The morphology, especially size of fish fry, is thought to influence predatory behavior (see Introduction). Graphed against total length, all behavioral changes (slopes of regressions), except the latency of group II, changed significantly with increasing size in both groups (regression analysis, regression equations in legends of Fig. 2).

Latency: Both groups had the same total length and latency at the beginning of the experiment. Although the latency of group I decreased significantly, with increase in total length, the latency of group II did not (Fig. 2A). The variance in both groups was considerable. The slopes were not significantly different (F = 2.49, p = 0.120).

Attempts in first 30 s: Throughout the experiment both groups had similar numbers of attempts during the first 30 s for a given total length (Fig. 2B). The slopes of both groups were homogeneous (F = 2.34, p = 0.131).

Attempts: The slopes of the regression equations were significantly different (F = 7.26, p = 0.009). In the beginning of the experiment fry of group II had for the same total length a smaller number of attempts (Fig. 2C). The increase in attempts with size may not be linear, the variation particular of small fish was considerable.

Weight: Both groups had the same weight-length relationship. The slopes are not different (F = 2.38, p = 0.127). Regression equations: (group I) weight = −0.48 + 2.98 × total length, r = 0.93; (group II) weight = −5.105 + 3.246 × total length, r = 0.98. The fry of both groups are therefore assumed to have been equally hungry and in equally good condition.

The Relative Importance of Age and Size on the Behavioral Response to Novel Prey

To evaluate the relative importance of age and total length on the response to novel prey I conducted three dummy variable regression analyses. Group was the

independent variable is held constant. An alternative analysis, an ANCOVA with two covariates (age and size), yielded the same results.

Latency: Overall the model was highly significant (F = 33.95, p < 0.000, adj. R^2 = 0.592). The age of the fish (t = −4.071, p < 0.000; b′ = −0.691) had a larger influence on the latency of the response of the fry than the total length (t = 2.07, p = 0.42; b′ = 0.370).

Attempts in first 30 s: Overall the model was highly significant (F = 38.88, p < 0.000; adj. R^2 = 0.629). Also for this behavioral variable age (t = 5.7, p < 0.000; b′ = 0.922) was the better predictor than total length (t = −1.5, p = 0.134; b′ = −0.259).

Attempts: Overall the model was highly significant (F = 35.1, p < 0.000, adj. R^2 = 0.601). Total length was not a good predictor of attempts judged by this model (t = 0.071, p = 0.943; b′ = 0.013). Age clearly accounted for the largest part of the variance in the dependent variable (t = 4.359, p < 0.000; b′ = 0.735).

Discussion

Fry of *Cichlasoma managuense* of group II showed significant behavioral improvements in their ability to deal with novel prey with increasing age (Fig. 1) and size (Fig. 2). The relative contribution of size and age to this improvement was not immediately obvious.

Behavioral allometry, behavioral changes that are correlated with size (FARR et al. 1986), may influence the behaviors that are correlated with capture success in the same direction as morphological improvements; they are closely correlated and are therefore hard to separate. In this study age of the fish (and the increased feeding experience with a different diet) had a larger influence on the improvement in predation behavior than size. In largemouth bass, COLGAN et al. (1986) also found that the level of experience explained more aspects of the improvement in predation efficiency than the size of the fish. Fisheries scientists, however, seem to favor length of the fish as the variable contributing most to the improvement in predation success of fish fry (ROSENTHAL 1969; HUNTER 1972, 1981; BLAXTER 1986).

The latency of group II fluctuated around 10 s and remained variable. This variability has been repeatedly reported in the literature (e.g. BRYAN & LARKIN 1972; RINGLER 1979; MEYER 1986, 1987). This variability may be the substrate for later specializations of individuals, i.e. some fish will switch to novel types of prey quickly, possibly turning into generalists compared to other fish that switch very reluctantly and thereby remain specialized.

With increasing age the number of attempts made in the two groups became more similar (the slope of group II is steeper, Figs. 1B, C and 2B, C), although the size difference persisted between the groups. This also supports the finding that age is more important than size for the fish's ability to respond to a novel prey stimulus. Other morphological improvements that may have contributed to the observed improvements in predation behavior e.g. the maturation of the visual system and the locomotory capabilities did probably occur but were not

documented in this study. These changes ought to be highly correlated with the size of the fish.

If the growth rate and the rate of maturation of the neural substrate were equal, then the differences in behaviors should have been constant between the groups because the size difference was constant. Latency, however, did not fit this pattern because the latency did not decrease with increasing size in group II (Fig. 2A). This difference in rate of change between the latency and attempts may be an indication of different rates of maturation of these parts of the predatory act or differences in the ability to transfer parts of the predatory behavior to novel prey. These assertions warrant further testing.

Maturation, and the ability to transfer feeding experience, are hard to separate and would require a number of prey-switching experiments with prey of varying similarity, because the fish must be fed (thereby gaining feeding experience) to grow and mature.

Provided that maturation, a change in behavior that is not influenced by experience, does not depend in any way on growth rate and temperature, then the problem of separating size from maturation may be tackled by raising groups of fish on the same diet but at different temperatures. That would produce different growth rates, thereby separating size and maturation experimentally.

Fish may develop a training bias (preference for a familiar type of prey) (WARE 1971; BRYAN & LARKIN 1972; BRYAN 1973) for one well-known prey. They also have to overcome this hindrance when new types of prey become abundant. Mature sticklebacks and rainbow trout need up to 50 trials until they start to feed on novel types of prey (BEUKEMA 1968; WARE 1971). On the other hand, older animals with more feeding experience may more quickly recognize new prey (see refs. in CURIO 1976).

Fry in this study were not given a choice between the novel and the familiar prey. Therefore, I did not test the strength of the training bias. Thus the possibility remains that fish did not develop a training bias for the manufactured diet and did not have to overcome it. GILLEN et al. (1981) reported that fish reared on manufactured diets had initially a lower capture success with fish prey than did fish reared on a more natural diet.

WELLS (1958, 1962) found that young Sepia first recognized their prey innately and the latency decreased with increasing age, whether or not the capture attempts were successful. This indicates that maturation can cause a decrease in latency. He also found that, correlated with the decrease in latency, the probability of attack on a variety of prey increased. The maturation in predatory behavior in Sepia was correlated with the development of a brain lobe that controls part of the predatory behavior. Nothing known about the development of the neural substrate in fish fry substantiates the shifts in the early ontogeny of predatory behavior.

Acknowledgements

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