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Prey Detectability Mediates Selectivity in a Zooplanktivorous Cyprinid (*Alburnus alburnus* (L.))

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Summary

To examine if prey choice in the bleak *Alburnus alburnus*, a planktivorous cyprinid of lake Neusiedler See, is affected by prey detectability, the foraging behaviour and selectivity in response to two cladoceran prey, *Leptodora kindti* and *Diaphanosoma mongolianum*, was investigated. In the field, bleak *Alburnus* showed negative selectivities for the smaller size-classes and a positive selectivity for the large size-classes of both prey types. Large *Diaphanosoma* are smaller and energetically less profitable, but are visually more conspicuous than *Leptodora* which possess a less pigmented body and relatively small compund eyes. Experiments with simultaneous provision of both prey types also showed such a selectivity pattern. When illumination was reduced, consumption rate decreased and no selectivity for either prey type could be found. When visibility of *Leptodora* was increased by means of artificial colouration, a positive selectivity for this prey type was recorded. A similar selectivity pattern happened in complete darkness, when vision was completely excluded. We conclude from this study that bleak selectivity is highly influenced by visual conspicuousness of their prey. When visual input is excluded and mechanical or chemical prey signals become more important, this pattern changes.

Key words: *Alburnus alburnus*, prey detectability, selectivity, *Diaphanosoma mongolianum*, *Leptodora kindti*.

Introduction

When in a given environment prey types differ among each other in detectability and size, predator sensory input will act as an important determinant of prey survival rates and thus contribute in shaping prey community structure. Studies on zooplanktivorous fishes (e.g., Zaret, 1972; Zaret and Kerfoot, 1975) were among the first ones to draw this conclusion that contrasts to the prediction of traditional foraging models that the energetically most profitable, largest prey types should be selected and finally eliminated (e.g., Hrbacek et al., 1961; Brooks and Dodson, 1965; Brooks, 1968). However, as predators obviously are non-omniscient, and profitable prey frequently manage to escape predation by reducing their detectability, foraging decisions usually do not follow simple energy-maximizing rules (Schluter, 1981; Stephens and Krebs, 1986; Sih, 1987).

Many zooplankters, for instance, possess highly transparent bodies which serve to increase their crypticity in the open water and limit shape and size recognition of fishes (Confer et al., 1978; McFall-Ngai, 1990). Increased crypticity lowers predator search rates (Gendron and Staddon, 1983) and may result in a preference of intensely pigmented smaller over less pigmented larger prey (Zaret, 1972; Zaret and Kerfoot, 1975; Kerfoot, 1982). Apart from this, differences in prey locomotion mode or movement intensity may influence fish food searching activity and prey selection to a considerable extent (Zaret, 1980; O'Brient et al., 1985; Ibrahim and Huntingford, 1989; Uiblein et al., 1992).

To forage successfully under different visibility conditions as well as in darkness, zooplanktivorous fishes frequently possess well developed eyes and lateral line systems (Lythgoe, 1978; Hairston et al., 1982; Montgomery and Macdonald, 1987; Kotrschal et al., 1991). In order to adequately determine the extent to which different sensorial mechanisms such as vision and mechanoreception contribute in prey search and detection and eventually affect prey selection in the field, respective feeding experiments with manipulation of prey visibility are required.

The bleak *Alburnus alburnus* (L.) is a zooplanktivore cyprinid which is one of the dominant fish species of the open water of Neusiedler See, a shallow eutrophic lake in eastern Austria (Herzig et al., 1994; Tatrai and Herzig, 1995). Earlier field studies have shown that bleak forage actively both during day and night with two cladoceran zooplankters, *Diaphanosoma mongolianum* and *Leptodora kindti*, forming the major diet components during summer (HERZIG, 1994; HERZIG et al., 1994). Significant differences in visual conspicuousness between the two prey types are found with respect to body size and pigmentation: *Diaphanosoma* have more pigmented, smaller bodies with large compound eyes. *Leptodora* have highly transparent bodies with small compound eyes. *Leptodora* shows somewhat more vigorous movements than *Diaphanosoma*, but both species show a relatively low activity level and may provide only weak mechanical stimulation.

In a recent field study on feeding behaviour of the razor fish *Pelecus cultratus* (L.), another planktivore cyprinid of Neusiedler See, adult *Diaphanosoma* were selected to a much higher extent than subadult *Leptodora*. The latter are larger-sized than the former ones, but visually less conspicuous with highly transparent bodies and smaller compund eyes (LIU and HERZIG, in press). In the present study, we addressed the following questions: Do bleak show a diet selection pattern similar to razor fish with high positive selectivity for adult *Diaphanosoma*? Does experimental manipulation of visual detectability of *Leptodora* and *Diaphanosoma* affect bleak foraging behaviour and selectivity?

Materials and Methods

Field Study

To study prey selectivity in Neusiedler See, bleak were caught by a gillnet (30 m × 1.5 m) between 10.00 and 13.00 h in July 1994. 19 individuals with full stomachs(10.3–13.5 cm SL) were killed immediately after capture and 4% formalin was injected into the body cavity in order to arrest digestion of the prey. Then the whole gut was removed, and the contents of the foregut was washed out, preserved in 4% formalin and analysed under a microscope. The number of prey items was counted for each food category. To determine the body size of the prey, the length of recognizable remains was measured, i.e. the length of the last segments of the second antenna of *Diaphanosoma mongolianum* and length of the furca of *Leptodora kindti*. Total body length of each prey individual was then estimated from linear relationships between the measurements of these parameters and corresponding lengths of individuals gathered from freshly collected plankton material (LIU and HERZIG, in press).

In order to assess selectivity with respect to differential prey type and body size, zooplankton samples were taken in parallel to the fish samples using a modified Schindler sampler. The plankton samples were counted, and the body length of each specimen of the two major prey *Diaphanosoma* and *Leptodora* was determined.

Both the gut and the field samples were separated into several size-classes. Because *Leptodora* were in all cases larger than *Diaphanosoma*, this also allowed a clear separation of the two prey types. For each size-class, selectivity was calculated using the electivity index D suggested by Jacobs (1974):

$$D_i = \frac{r_i - p_i}{r_i + p_i - 2r_ip_i}$$

where D_i is the electivity index for size class i, p_i is the proportion of individuals belonging to size-class i in the lake and r_i is the proportion of that size-class in the guts. Values of D_i range from -1 to 1; 0 would indicate random feeding while $D_i > 0$ and $D_i < 0$ indicate either positive or negative selectivity by the fish, respectively.

Experimental Study

A total of 30 bleak (9.5–10.5 cm SL) from Neusiedler See were kept in large holding tanks (90 × 50 × 35 cm) in the laboratory for a period of eight weeks and were fed a mixture of zooplankton prey twice daily. Temperature was kept at 20 ± 1°C and light was controlled at a 12L/12D cycle.

Adult living *Diaphanosoma mongolianum* (1.15 ± 0.06 mm body length) and subadult living *Leptodora kindti* (3.31 ± 0.57 mm body length) from fresh zooplankton samples of Neusiedler See were used as experimental prey.

In each of five different experiments, ten fish were tested individually and independently of each other. For the experiments, an experimental tank (40 × 25 × 30 cm) filled with 151 water was used. The tank was surrounded by white styropor walls leaving a small window for observation. Illumination was provided by a fluoresent tube from above with adjustable light intensity. In preceding training sessions all fish had been accustumed to the experimental conditions to exclude potential behavioural modification through learning.

Each individual fish had been starved for 24 h before being transferred into the experimental tank where it was enclosed in one corner of the tank by a plastic partition. Then 100 individuals of both prey were introduced and well distributed in the tank. The experiments started when the partition was removed and the fish had free access to the prey. Each experiment lasted for a period of 15 min. Afterwards, the fish were netted and the remaining prey were counted. In a training phase prior to the experiments, this method had been optimized so that the experimenter was able to determine the number of prey consumed with great precision.

In the first two experiments, light level was altered to examine the effect of reduced illumination on foraging behaviour and selectivity. In the first experiment, light level was kept at 600 lx and in the second at 15 lx. In the following two experiments, one of the two prey types was artificially coloured to determine the effect of prey visual conspicuousness on choice behaviour. Colouration was achieved by soaking the prey in brown, commercially available food dye for a period of 15 min. After this treatment, both cladocerans were still alive and did not show any behavioural changes. In the third experiment with a light level of 600 lx coloured *Leptodora* were used. In the fourth experiment with a light level of 15 lx, *Diaphanosoma* had been coloured and *Leptodora* were left uncoloured. In the last experiment, the two cladoceran species were presented in total darkness to examine the ability of the fish to detect prey by non-visual cues only.

For statistical comparisons of prey consumption rates among the five different experiments one-way ANOVA followed by a Scheffe multiple range test ($p < 0.05$) was used. To determine prey selectivity, the electivity index D was calculated. A two-tailed Student's t-test (ZAR, 1984) was employed to detect significant deviations in the electivity index from 0 which would indicate that positive or negative selectivity had occurred (JOHNSTON and MATHIAS, 1994). Because only a single size-class of each prey type was provided in the experiments, a positive selectivity for one prey type would imply a negative selectivity for the other and vice versa. Consequently, the electivity index was calculated only for *Leptodora*.

Results

The selectivity of bleak for different size classes of *Diaphanosoma mongolianum* and *L. kindti* in Neusiedler See is shown in Fig. 1. For *Diaphanosoma*, a negative selectivity for length classes from between 0.40 mm and 0.79 mm and a positive selectivity for length classes 0.80 to 1.33 mm was found. For *Leptodora*, length classes between 1.72 mm and 4.99 mm were negatively selected and length classes between 5.0 mm and 12.0 mm were positively selected. Accordingly, bleak selected adult *Diaphanosoma* over subadult *Leptodora*, although the latter have larger bodies and are energetically more profitable.

The consumption rates for either prey species as well as the total consumption rate varied significantly among the five different experiments (*Diaphanosoma*: $F(4,45) = 26.1$, $p < 0.001$; *Leptodora*:

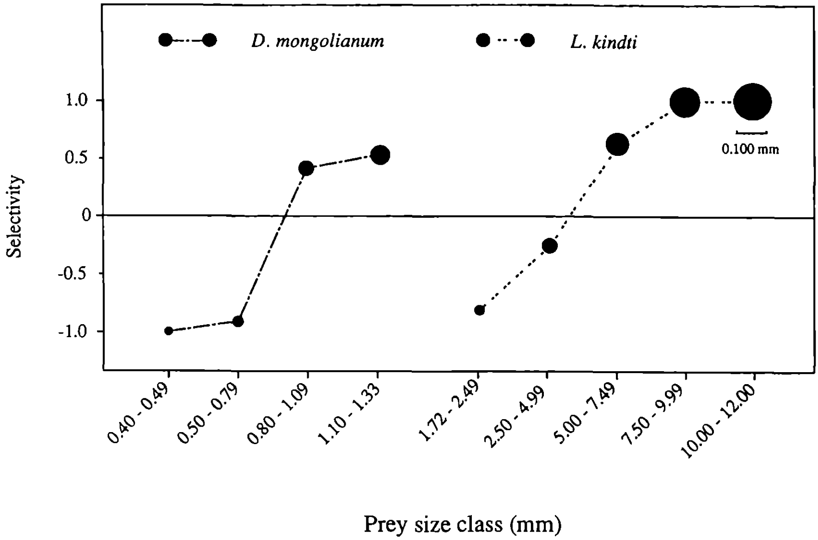

Fig. 1. Selectivity of bleak *Alburnus alburnus* for different size classes of *Diaphanosoma mongolianum* and *Leptodora kindti* expressed by the electivity index *D*. The size of each dot indicates the mean size of the compound eye of the respective size-class

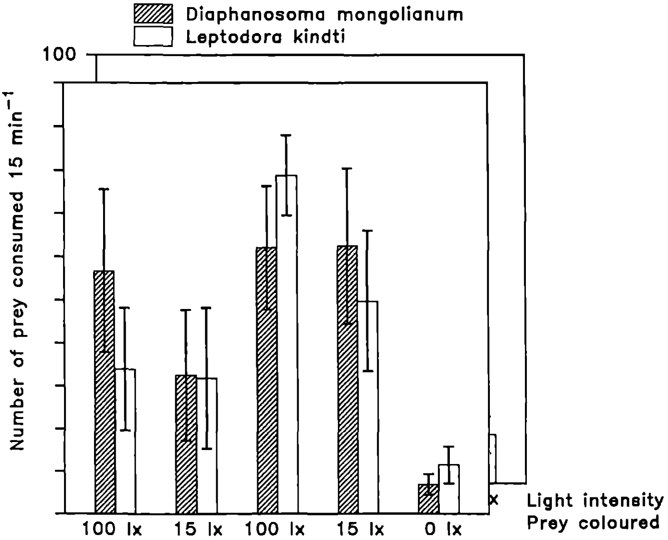

Fig. 2. Prey consumption rate of bleak measured as the number of prey consumed per 15 min in five successive experiments with provision of different light intensities and/or artificially coloured prey

F(4,45) = 37.1, $p < 0.001$; total: F(4,45) = 32.9, $p < 0.001$; Fig. 2). For *Diaphanosoma*, the highest consumption rates were achieved in the first experiment with high light level and in the two experiments with presentation of coloured prey. The lowest consumption rate occurred in total darkness. For *L. kindti*, the highest consumption rate was found in the third experiment with provision of coloured *Leptodora* and the lowest in the darkness experiment. With respect to total consumption rate, significantly lower values were recorded in the darkness experiment compared to all others. In the experiment with presentation of coloured *Leptodora* total consumption rate was highest and differed significantly from the three experiments with provision of uncoloured prey. The multiple range analysis also showed that in the experiment with presentation of coloured *Diaphanosoma* at low light level were significantly higher than in the second experiment when both prey types had been offered without artificial colouration at low light level.

In the first experiment with high light level, bleak showed a significant negative selectivity for *Leptodora* ($t = 6.1, p < 0.001$; Fig. 3). The electivity index did not significantly deviate from 0 in the second experiment with low light level ($t = -0.5, p > 0.5$) indicating random selection of either prey type. In the third experiment with presentation of coloured *Leptodora*, bleak showed a significant positive selectivity for this prey type ($t = 3.9, p < 0.005$). In the fourth experiment with coloured *Diaphanoso-*

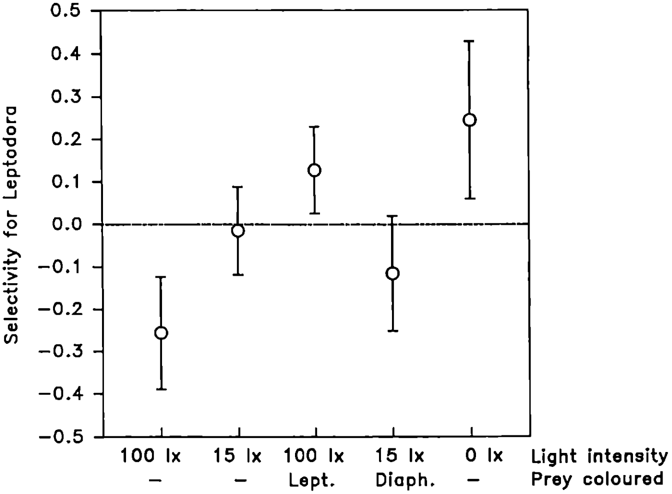

Fig. 3. Selectivity (electivity index *D*) of bleak for *Leptodora kindti* in five successive experiments with provision of different light intensities and/or artificially coloured prey

ma, a significant negative selectivity for *Leptodora* was found ($t = -2.7$, $p < 0.025$). In total darkness, bleak showed a highly significant positive selectivity for *Leptodora* ($t = 4.2, p < 0.005$).

Discussion

In Neusiedler See, bleak show negative selectivity for smaller and a positive one for larger size-classes of *Diaphanosoma mongolianum* and *Leptodora kindti*. Adult *Diaphanosoma* were positively selected by the fish, although they are energetically less profitable with shorter and lighter bodies containing less dry weight than subadult *Leptodora*. These results point to the existence of certain constraints acting upon prey selection.

As shown by the experiments, changes in visual conspicuousness of either prey type influence bleak foraging activity and selectivity considerably. When light intensity remained at high level or when visual conspicuousness of the prey was increased by artificial colouration, consumption rate clearly increased. Additional observations of feeding behaviour during the four experiments in light showed that prey capture efficiency remained at high level throughout. With increasing their consumption rates, the fish obviously adopted a higher search velocity. Search rate increase with improved detectability (GENDRON and STADDON, 1883). Earlier experimental investigations on the foraging responses of cyprinid fish to gammarid prey with differential mobility levels suggested that total search rate increases significantly with improved prey detectability (UIBLEIN et al., 1992).

Selectivity pattern in light was as predicted: the higher conspicuous prey was positively selected. In the experiment with both uncoloured prey at low light level, no selectivity was observed indicated increased difficulties to dirscriminate visually among the two prey types. With this respect it would be interesting to examine the effects of turbidity (TATRAI and HERZIG, 1995).

In darkness, the consumption rate was considerably reduced indicating that foraging success in bleak is highly dependent on vision. However, these results also suggest that bleak is able to shift from a visually oriented to a non-visual, mechanically or chemically guided search behaviour when visual sensory input is completely absent. Interestingly, *Leptodora* became the preferred prey under these conditions. This may reflect the adoption of a selectivity critierion based exclusively on mechanical signals from the prey. *Leptodora* as the larger and more vigorously moving prey should produce a higher amount of water displacement thus facilitating prey detection by the lateral line organs (DIJKGRAAF, 1962; LYTHGOE, 1978).

Our findings support the conclusion of earlier workers that high transparency in zooplankton provides an effective antipredator strategy, especially in combination with reduced size of visually conspicuous body structures such as compound eyes (ZARET, 1972; ZARET and KERFOOT, 1975; HESSEN, 1985). Although cladocerans mainly use a tactile search mode during foraging (e.g., HERZIG and AUER, 1990), compound eyes may have considerable functional value for proper vertical orientation and behavioural adjustments in well illuminated waters (e.g., YOUNG and GETTY, 1987) and have been retained in many zooplankters though an increase in their overall visual detectability. Large adults of *Leptodora* have much larger compound eyes than *Diaphanosoma* and thus should be at highest risk. *Leptodora* is a voracious predator with the larger size classes feeding on subadult *Diaphanosoma* at particular high rates (HERZIG and AUER, 1990; HERZIG, 1994). In Neusiedler See, prey selection by bleak and other zooplanktivorous fishes should therefore have considerable direct and indirect impacts on zooplanktion composition and density with lower mortality rates in the smaller size-classes of the two cladoceran species.

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