

# Effect of prey size on the estimation of behavioral visual resolution of bluegill (*Lepomis macrochirus*)

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**Abstract:** Unlike larger conspecifics (>35 mm SL), behavioral visual resolution of young-of-the-year bluegill (*Lepomis macrochirus*) (11–32 mm SL) measured as visual angle is not independent of prey size. Visual angles based on the maximum location distances (MLDs) for bluegill  $\leq 32$  mm SL increased directly with prey size and differed significantly among three prey size categories (*Daphnia pulicaria*: carapace length 2.3, 1.1, and 0.8 mm). Visual angles of small bluegill viewing their preferred prey were approximately half those for fish viewing the largest prey and indicate that the behavioral visual resolution of small bluegill was previously underestimated. Errors in prey size measurements have a much larger effect on visual angle than do errors in reaction distance. In most instances, MLDs of small bluegill to large prey were significantly longer than were MLDs to small- and medium-sized prey. MLDs for the smallest prey were about 70% those for the largest prey; the difference between the MLDs within a fish size category is much less than predicted if visual angle is independent of prey size. Poor visual and locomotory capabilities of small bluegill probably contribute to the comparatively small differences in reaction distances to small versus large prey.

**Résumé :** À la différence de ce qu'on observe chez les conspécifiques de plus grande taille (>35 mm LS), la résolution visuelle comportementale des jeunes de l'année de crapet arlequin (*Lepomis macrochirus*) (11–32 mm LS) mesurée en tant qu'angle visuel, n'est pas indépendante de la taille des proies. Les angles visuels calculés à partir des distances maximales de localisation (MLD) pour les crapets  $\leq 32$  mm LS augmentent directement en fonction de la taille des proies et diffèrent de façon significative entre trois catégories de taille des proies (*Daphnia pulicaria* : longueur de carapace de 2,3, 1,1 et 0,8 mm). Les angles visuels des petits crapets observant leur proie favorite étaient inférieurs de moitié environ à ceux des poissons observant les proies les plus grosses, ce qui indique qu'on a jusqu'à maintenant sous-estimé la résolution visuelle comportementale des petits crapets. Les erreurs dans les mesures de la taille des proies ont un effet beaucoup plus grand sur l'angle visuel que les erreurs dans la distance de réaction. Dans la plupart des cas, les MLD des petits crapets par rapport aux proies de grande taille étaient significativement plus longues que les MLD par rapport aux proies de taille petite et moyenne. Les MLD par rapport aux proies les plus petites correspondaient à environ 70 % de celles observées avec les proies les plus grosses; la différence entre les MLD au sein d'une catégorie de taille de poissons est nettement inférieure à celle qui serait prévue si l'angle visuel était indépendant de la taille des proies. Les faibles capacités visuelles et locomotrices des petits crapets ont probablement un effet sur les différences comparativement faibles dans les distances de réaction à l'égard des proies de petite taille et de grande taille.

[Traduit par la Rédaction]

## Introduction

Understanding the role of visual resolution in predator-prey interactions has important implications for testing foraging and community-level models for freshwater and marine systems. The retina of a teleost fish grows throughout the animal's lifetime (Müller 1952; Johns and Easter 1977; Hairston et al. 1982; Easter 1992) and the changing visual capabilities of fish are central to the estimation of encounter probabilities required

for most diet choice and habitat switching models where the effective availability of prey in the environment is a function of visibility (Werner and Hall 1974, 1988; O'Brien, 1979; O'Brien et al. 1976; Mittelbach 1981, 1984; Eggers 1982; Aksnes and Giske 1990, 1993). Young-of-the-year are typically the most abundant age-class of fish populations (Beard 1982) and can potentially play an important role in structuring zooplankton communities through size-selective predation. Ontogenetic changes in the visual system will greatly influence prey detection ability (Baerends et al. 1960; Blaxter 1975; Otten 1981; Hairston et al. 1982; Breck and Gitter 1983; van der Meer and Anker 1984; Li et al. 1985; Fernald 1988; Sivak 1990; Walton et al. 1994) and it is clear that while retinal growth is central, another unidentified factor plays a critical role when fish are small.

Behavioral and anatomical measures of visual resolution that are highly correlated in bluegill (*Lepomis macrochirus*) >30 mm standard length (SL) (Hairston et al. 1982; Breck and Gitter 1983; Li et al. 1985) are less strongly correlated in small sunfish (<20 mm SL; Walton et al. 1994). The lower extent of association between behavioral and anatomical measures of

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visual resolution indicates that, in addition to ontogenetic changes of cone cell spacing and lens focal length, other factors influence the prey detection abilities of small bluegill. Prey detection by small bluegill foraging on 2-mm *Daphnia* requires images that are greater than two times the average intercone spacing on the retina, and the proportion of prey detections with an image size greater than twice the intercone interval declines with increasing fish size (Walton et al. 1994). Such behavioral observations suggest that the image of the prey on the retina might be blurred in very small sunfish; comparatively poor lens quality, inadequate accommodative mechanisms that move the lens and focus the image on the retina, or lower neuronal connectivity (Blaxter 1975; Wagner 1978; Otten 1981; Fernald 1988; Sivak 1990) might cause the blurred images. Cognitive factors, such as learning (Meyer 1986), prey recognition (Hughes 1979), and prey size selectivity, might also affect the size-related changes of behavioral visual resolution. Our study examines the effect of prey size on estimates of behavioral visual resolution for bluegill foraging on crustacean prey (*Daphnia pulicaria*).

## Materials and methods

Bluegill larvae were collected off a nest in Rainbow Springs Lake, Waukesha County, Wis., U.S.A., and reared in the laboratory on daily additions of a mixed assemblage (i.e., *Synchaeta* spp., *Polyarthra* sp., *Asplanchna* sp., *Bosmina longirostris*, *Ceriodaphnia* sp., *Leptodiatomus ashlandi*, and *Diaacyclops thomasi*) of nearshore Lake Michigan zooplankton. Juvenile bluegill (>25 mm SL) were caught with a seine in Lulu Lake (Walworth County, Wis.) and maintained in the laboratory on a daily ration of Lake Michigan zooplankton and freeze-dried *Tubifex* worms.

Experiments were carried out in an observation tank (bottom dimensions 21 × 14 cm; water depth 2 cm) with a grid of 1-cm squares that was affixed to a sheet of white Plexiglas on the bottom of the aquarium. To determine the visual angles for bluegill >18 mm SL where reaction distances might approximate, or exceed, the dimensions of the small aquarium, the reaction distances were measured in a larger aquarium (bottom dimensions 60 × 30 cm) at a water depth of 4 cm. The aquaria were wrapped with white paper to minimize distractions and provide the fish a uniform visual background. Illumination was provided by three 40-W warm-white fluorescent lamps ( $\lambda_{\text{max}} = 550 \text{ nm}$ ) giving ambient light levels at the water's surface of  $4.32 \mu\text{einsteins}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ .

Prey detection by bluegill is indicated by a reorientation of the long axis of the body towards the prey (Vinyard and O'Brien 1976). Reorientation is typically followed by rapid swimming to the location of the prey and capture. Reaction distance is defined as the distance between predator and prey at which the predator exhibits this characteristic orientation behavior. Visual angle is defined as the angle at the fish's eye subtended by the prey at detection and is a function of prey size and the reaction distance.

The reaction distances of bluegill were measured from videotapes of fish foraging. The video camera was positioned 88 cm above the water's surface. Three fish of similar size were placed into the observation tank because individual fish were skittish and did not readily feed. The observer watched the fishes' behavior on a television monitor that was positioned outside the visual field of the fish. Laboratory-reared *Daphnia* were sieved and then sorted by hand into three size categories (mean lengths ± SE:  $0.76 \pm 0.03$ ,  $1.1 \pm 0.1$ , and  $2.3 \pm 0.1 \text{ mm}$ ). For each observation period, the body size either of a representative sample ( $N = 25\text{--}30$  individuals) for each prey size-class or of individuals was measured, separated by body size into tissue culture wells, and then used in the experiments. Individual prey were placed into the aquarium by a pipet at a position in the tank opposite

that occupied by the fish. Sham introductions were routinely done to avoid the fish associating the pipet with food. Reaction distance ( $d$ ) was measured by calculating the distance between the  $x,y$ -coordinates of the fish's head at orientation to the prey and at the attack on the prey. The visual angle ( $\theta$ ) was calculated as

$$(1) \quad \theta = 2 \tan^{-1} (h/2d)$$

where  $h$  is prey size. Hairston et al. (1982) assumed that prey size was equivalent to the average diameter of a sphere having the same volume as an oblate spheroid with its major axis being *Daphnia* length and width and its minor axis equal to *Daphnia* thickness; prey size is equal to the carapace length multiplied by 0.64. This proportion also approximates the fraction of the *Daphnia* carapace length (excluding the tail spine) that is occupied by the pigmented digestive tract.

The maximum location distance (MLD) is a better behavioral measure of visual capabilities than is the mean reaction distance for fish that use a saltatory search strategy (O'Brien et al. 1990). The MLD is the outer boundary of the distribution of pursuit length within which 90% of the pursuits fall (O'Brien and Evans 1991). The MLD was calculated using the longest 10% of the reaction distances for each prey size – fish length category.

The angle subtended by the prey at the fish's eye at the moment of detection was compared among the three *Daphnia* size categories across the range of fish size-classes by ANCOVA using ln-transformed SL as a covariate. To satisfy the assumptions for a straight-line ANCOVA model, visual angles were also ln-transformed prior to analysis. For each prey size category, visual angles for the entire range of bluegill were then examined quantitatively by transforming SL to natural logarithms and fitting ln-transformed visual angle to this variable using least squares linear regression. Only visual angles calculated from the longest 10% of the reaction distance distributions for each of the prey size – fish length categories were used in these analyses.

To examine how prey selectivity of bluegill changes as fish grow, we compared prey selection with that expected from random encounters of fish with zooplankton prey. Preference is any deviation from random sampling of the prey (Chesson 1983). The preference measure,  $\alpha_i$  (Chesson 1983), was calculated as

$$(2) \quad \alpha_i = \frac{r_i/n_i}{\sum_{j=1}^m r_j/n_j}, \quad i = 1, \dots, m$$

where  $n_i$  is the expected number of prey type  $i$  present in the diet assuming random encounters with the prey and  $r_i$  is the number of items of food type  $i$  in the diet. In contrast with the reaction distance experiments where individual prey were used, prey densities in the prey selection experiments ranged from 9 to  $20\cdot\text{L}^{-1}$ . The expected diets for each fish size category (11, 14, 16, 29, 38, 60, and 76 mm SL) studied by Li et al. (1985) and Walton et al. (1992) were computed using Wetterer and Bishop's (1985) model for prey selection based on apparent size. The expected distributions of attacks were corrected for truncation of the visual field by shallow water depth using  $2\pi a(d^2 - a^2/3)$  (Werner and Hall 1974) where  $d$  is reaction distance and  $a$  is equal to one half the depth of the experimental environment.

## Results

The visual angles of bluegill for all prey size categories decreased nonlinearly with increasing fish size (Fig. 1) and were directly related to prey size (Table 1). Visual angles for bluegill viewing different-sized prey differed significantly (ANCOVA of prey size on ln-transformed  $\theta$  using ln-transformed SL as the covariate; prey size:  $F_{2,97} = 142.4$ ,  $P < 0.0001$ ; homogeneity of slopes:  $F_{2,95} = 0.363$ ,  $P > 0.697$ ). Behaviorally determined visual angles for bluegill between 11 and

32 mm SL decreased by 52 and 103 minutes of arc for the smallest and largest prey size categories, respectively, used in our experiments.

Visual angles based on the MLD differed significantly among the prey size categories, with greatest detection capability for the smallest prey (Table 1). The difference in visual angle between the small and large prey size categories is approximately 50% (mean  $\pm$  SE:  $0.50 \pm 0.11$ ). Visual angles for 25-mm fish differ from this trend; however, the calculations are based on only two observations per prey size category.

For each bluegill size category, MLD increased directly as a function of prey size (Table 1). MLDs within a particular bluegill size category to the smallest prey were on average 71% of those for the largest prey ( $MLD_{small\ prey}/MLD_{large\ prey}$ , mean  $\pm$  SE:  $0.71 \pm 0.13$ ). Reaction distances of bluegill to the largest prey were significantly longer than to small- and medium-sized prey (Tukey's HSD;  $P > 0.05$ ). MLD increased by approximately 12-fold as bluegill grew from 11 to 32 mm SL.

Even though the ratio of the mean reaction distance to small versus large prey ( $RD_{small\ prey}/RD_{large\ prey}$ , mean  $\pm$  SE:  $0.70 \pm 0.08$ ) was similar to that for the MLD, mean reaction distances of bluegill  $>25$  mm SL differed significantly among prey size categories (Tukey's HSD;  $P < 0.05$ ) (Table 1). For bluegill  $\leq 25$  mm SL, mean reaction distance did not differ significantly among prey size categories (Table 1). In contrast with the mean reaction distance, the MLD for the largest and smallest prey differed significantly for 75% of the fish size-classes examined.

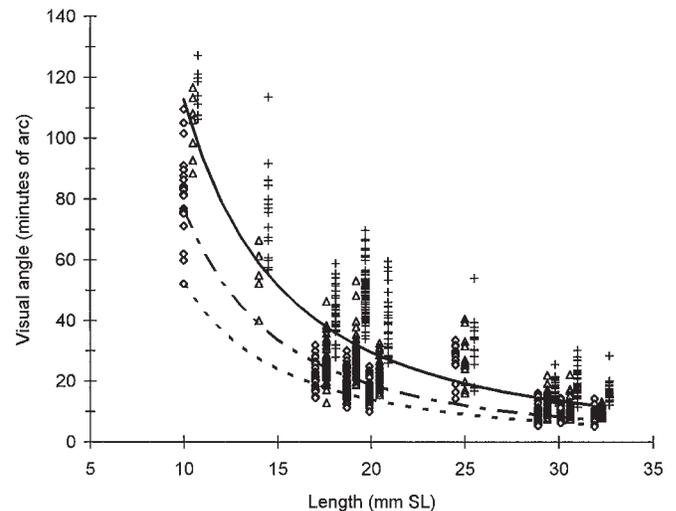
The mean reaction distance, the minimum reaction distance, and the variance around the mean reaction distance increased directly with fish size (Fig. 2). The reaction distances of 11-mm bluegill ranged narrowly from 1 to 5 cm whereas the reaction distances of 30- to 32-mm bluegill ranged broadly from 11 to 46 cm.

Prey selection by the three smallest and two largest bluegill size-classes differs significantly from that predicted from random encounters with prey ( $\chi^2$  tests;  $P < 0.05$ ,  $df = 2$ ). Bluegill  $\leq 16$  mm SL select significantly more small prey, and fewer intermediate and large prey, than expected from prey visibility (Fig. 3). Preference values of bluegill  $<16$  mm SL were high ( $\alpha_i > 0.7$ ) for small prey and low ( $\alpha_i < 0.2$ ) for intermediate and large prey. Conversely, bluegill  $\geq 60$  mm SL preferentially chose the largest *Daphnia* and consumed fewer small prey than is expected from random encounters. *Daphnia* of intermediate size were attacked as encountered ( $\alpha_i$  between 0.3 and 0.35). Prey selection by bluegill of intermediate size (29.3 and 38 mm SL) did not differ significantly from that expected on the basis of random encounters with prey ( $\chi^2$ ;  $P > 0.05$ ,  $df = 2$ ); preference values of intermediate-sized bluegill for the three prey size categories were comparatively similar to those of smaller and larger conspecifics (Fig. 3).

## Discussion

The independence of visual angle from prey size is essential when making intraspecific (i.e., among fish size-classes) or interspecific comparisons of the behavioral visual resolution of fish where the prey size used in experiments differs (Wanzenböck and Schiemer 1989; Browman et al. 1990; Wanzenböck 1992; Wahl et al. 1993; Walton et al. 1994). Behaviorally

**Fig. 1.** Behaviorally based estimates of visual resolution of juvenile bluegill as a function of fish SL. The visual angles were calculated from reaction distances of fish ( $N = 36$ ) to three sizes of *Daphnia*: small ( $\sim 0.8$  mm, diamonds), medium ( $\sim 1.1$  mm, triangles), and large ( $\sim 2.3$  mm, plus signs). The data for each fish size are spread out horizontally to facilitate illustration. Least squares regressions of visual angle,  $\theta$ , in minutes of arc for the longest 10% of the reaction distances (MLDs) for a particular prey size – fish size-class category on fish length (SL) in millimetres for each prey size category are shown: small prey (dotted curve),  $\ln \theta = 8.33 - 1.90 \ln SL$  (SE of slope = 0.12,  $N = 33$ ,  $F = 248.81$ ,  $P < 0.0001$ ); medium prey (dashed-dotted curve),  $\ln \theta = 8.99 - 2.02 \ln SL$  (SE of slope = 0.11,  $N = 34$ ,  $F = 318.58$ ,  $P < 0.0001$ ); large prey (solid curve),  $\ln \theta = 9.17 - 1.93 \ln SL$  (SE of slope = 0.06,  $N = 34$ ,  $F = 895.46$ ,  $P < 0.0001$ ).



determined visual angles are of similar magnitude for a particular fish size-class reacting to prey of the same apparent size, provided that prey do not exhibit size-related differences in coloration, movement patterns, and morphology. The visual angle subtended by the prey at detection is independent of prey size in bluegill  $>30$  mm SL (Hairston et al. 1982; Breck and Gitter 1983; Li et al. 1985). Visual angles were calculated using the mean or median reaction distance in the aforementioned studies on bluegill (Hairston et al. 1982; Breck and Gitter 1983; Li et al. 1985); visual angles based on the MLD for bluegill  $>45$  mm SL do not differ appreciably among prey size categories (see Hairston et al. 1982). For bluegill  $\leq 45$  mm SL (Hairston et al. 1982), visual angles based on the MLD differ among prey size categories; although visual angles for fish viewing small prey tend to be smaller than for the largest prey, the differences are not strongly related to the *Daphnia* size categories. The data presented here indicate that behaviorally determined visual angles of small bluegill ( $\leq 32$  mm SL) are not independent of prey size.

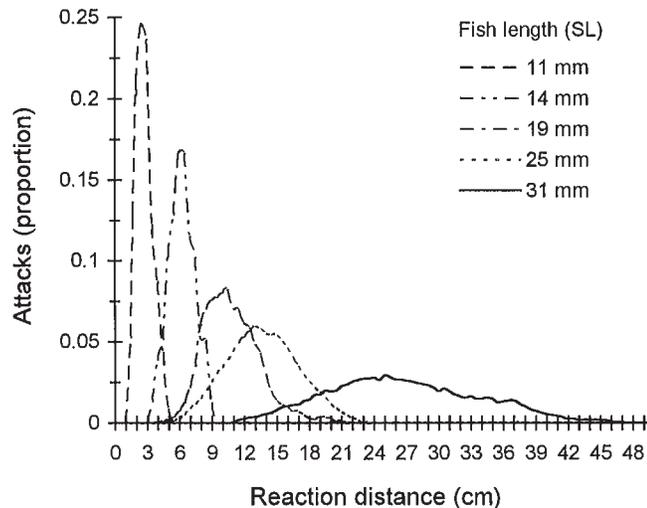
Because visual angle increases directly as a function of prey size, visual resolution of small fish will be underestimated when large prey are used in behavioral experiments. Visual resolution is inversely related to visual angle. To discern individual *Daphnia* and reduce errors caused by parallax in the estimation of reaction distance during the analysis of videotapes (i.e., use of a long working distance between the video

**Table 1.** Ontogenetic change in the visual angles based on the MLDs and mean reaction distances of bluegill (SD in parentheses).

SL (mm)	N (S, M, L)	Visual angle ( $\theta$ , minutes of arc)			MLD (cm)			Mean reaction distance (cm)		
		Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
11	3, 2, 2	58.0 (5.2) a	90.6 (3.0) b	116.9 (1.0) c	2.2 (0.4) a	2.2 (0.1) a	3.5 (0.1) b	1.8 (0.5) a	1.8 (0.3) a	3.0 (1.4) a
14	—, 1, 3		39.9	58.0 (1.6)		6.2	7.4 (0.2)		7.0 (1.5) a	9.7 (0.8) a
18	4, 5, 4	15.9 (1.2) a	20.2 (1.3) b	30.7 (1.9) c	10.8 (0.8) a	14.0 (2.9) ab	15.2 (1.0) b	7.9 (1.6) a	9.7 (2.4) a	11.0 (2.2) a
19	10, 7, 7	13.2 (1.2) a	18.0 (3.2) b	37.1 (2.1) c	13.1 (1.2) a	13.4 (0.8) a	13.7 (0.8) a	9.2 (2.0) a	9.4 (1.8) a	10.5 (2.0) a
20	4, 4, 4	11.5 (1.1) a	16.7 (1.0) b	27.5 (1.0) c	14.9 (1.5) a	15.3 (1.0) a	18.6 (0.7) b	10.6 (2.5) a	11.2 (2.1) a	13.2 (3.3) a
25	2, 2, 2	13.4 (1.5) a	16.6 (0.7) a	17.4 (0.8) a	8.7 (0.3) a	13.2 (0.6) b	16.9 (1.2) c	7.8 (1.0) a	8.6 (2.7) a	11.5 (4.1) a
30	4, 4, 4	6.0 (0.4) a	8.1 (0.7) b	13.3 (0.6) c	29.9 (1.9) a	31.5 (2.5) a	40.0 (1.6) b	19.0 (5.7) a	22.2 (5.6) a	32.3 (5.4) b
31	4, 4, 4	6.6 (0.3) a	8.3 (0.6) b	12.7 (1.1) c	25.9 (1.0) a	30.4 (2.3) a	41.6 (3.7) b	18.4 (4.4) a	22.9 (5.1) b	28.4 (7.2) c
32	5, 4, 4	6.4 (0.9) a	8.2 (0.3) b	13.5 (1.1) c	29.1 (4.0) a	30.0 (1.0) a	39.4 (3.2) b	20.5 (4.0) a	24.6 (3.2) b	31.9 (4.7) c

**Note:** N is the sample size for calculations of visual angle and the MLD where S, M, and L are the number of observations for small, medium, and large prey size categories, respectively. Visual angles, MLDs, or mean reaction distances for the three size-classes of *Daphnia* followed by the same letter do not differ significantly (Tukey's HSD;  $P > 0.05$ ) within a particular fish size category.

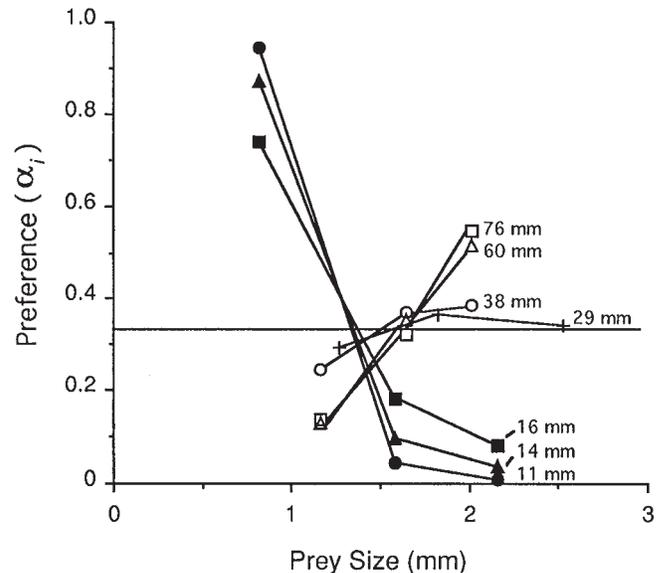
**Fig. 2.** Distribution of reaction distances among bluegill size categories. The distributions are moving averages of three (bluegill  $\leq 20$  mm SL) or 10 points (bluegill  $> 20$  mm SL) for equivalent numbers of attacks on the three prey size categories. The reaction distances for 18- to 20-mm bluegill are summed and plotted as 19 mm. The reaction distances for 30- to 32-mm bluegill are summed and plotted as 31 mm.



camera and the fish), large prey (2-mm *Daphnia*) were used in reaction distance trials by Walton et al. (1994). The visual angles for all bluegill to the largest *Daphnia* used here are of comparable magnitude with those reported by Walton et al. (1994); however, the results presented here indicate that the behavioral visual resolution of small bluegill was previously underestimated by approximately twofold (Fig. 1).

The difference in visual angles across the fish size-classes used here for the smallest and largest prey size categories is approximately 50%. It is unlikely that measurement errors caused a nearly 50% difference in visual angles for fish within a particular size-class viewing the smallest versus the largest prey. The magnitude of errors in visual angle is inversely related to prey size and reaction distance. Errors in prey size measurements have a much greater effect on visual angle estimates than do errors in reaction distance. If prey size is under- or overestimated by 0.1 mm, then the error in visual angle

**Fig. 3.** Change in prey preference ( $\alpha_i$ ) of bluegill during growth. The preferences of fish in six size-classes offered three sizes,  $i$ , of *Daphnia* are illustrated. Preference values were calculated from data reported in Li et al. (1983) and Walton et al. (1992).  $\alpha_i = 0.33$  is the value for no selectivity; above this value, prey are attacked in greater proportion than encountered and below this value are attacked in lesser proportion than encountered.



using the smallest prey size category is approximately three times larger than when using the largest prey. When 0.79-mm prey are used in experiments, visual angle changes by approximately  $13\% \cdot 0.1 \text{ mm}^{-1}$ . If 2.34-mm prey are used, visual angle changes by only  $4\% \cdot 0.1 \text{ mm}^{-1}$ . At visual angles of  $58'$ , a 0.1-mm error in the size of small prey changes visual angle by  $7.3'$  whereas a similar error in the size of large prey changes visual angle by  $2.5'$ . Errors in reaction distance of 0.1 cm change visual angle by a comparatively small and decreasing amount as visual angle declines. This difference is only about 3 and 1% for small and large prey, respectively, when visual angle is  $58'$  and  $< 1\%$  for both prey categories when visual angle is  $< 13'$ .

Several aspects of our experimental conditions may not duplicate natural conditions, but as long as the effects are equivalent

across prey size categories, our conclusions regarding the effects of prey size on estimates of behavioral visual resolution should remain unchanged. The cues commonly used by visual predators for prey recognition include size, movement, and shape (McFarland 1985). The probability that a prey will be detected by a predator is influenced by its angular size and velocity, the degree of contrast with the background, and the general level of illumination (McFarland 1985). Fluorescent lights do not duplicate the distribution and range of electromagnetic spectral components found in nature or provide all wavelengths (e.g., near ultraviolet) possibly used by fishes to detect prey (Cameron and Pugh 1991; Guthrie and Muntz 1993). The white background used in our experiments is likely to enhance prey visibility relative to that under natural conditions where the contrast between the background and the prey is less. Visual angles based on the MLD (Table 1) are by definition smaller than those reported previously based on the mean or median reaction distance to prey of equivalent size (Hairston et al. 1982; Breck and Gitter 1983; Li et al. 1985). Yet, visual angles calculated using the mean reaction distance for 30- to 32-mm SL fish (~18', Table 1) are still smaller than those of 37-mm SL bluegill (27') used by Hairston et al. (1982). Visual angles (calculated using the MLDs) of 30- to 32-mm SL bluegill viewing a 0.8-mm *Daphnia* were nearly 6' (Table 1) and approach the minimum visual angle found among aquatic predators. Guthrie and Muntz (1993) found that aquatic predators (i.e., fish, marine mammals, and cephalopods) do not have visual acuities better than 4' and suggested that visual acuity better than 4–5' serves no useful purpose in aquatic environments where high spatial frequencies (i.e., the fine detail of objects being viewed) are heavily attenuated.

To date, planktivorous fish have not been shown to estimate absolute prey size; yet, prey selection often differs from that predicted by apparent size alone (Fig. 2). Wetterer (1989) suggested that sunfish use apparent size to direct their attention to a prey item when prey encounters are simultaneous and then evaluate actual prey size. Ewert and Burghagen (1979) found that at about 2 weeks after metamorphosis, midwife toads (*Alytes obstetricans*) use apparent size to judge prey size and that 6 months later, toads make prey size judgments independently of the visual angle. Object size constancy has also been observed other anurans (*Rana pipiens* (Ingle 1968) and *Bufo bufo* (Ewert and Gebauer 1973)). To estimate absolute prey size, fish must use retinal size and an estimate of distance. Several mechanisms for how fish perceive distance have been suggested: parallax while moving through the water (assumes sunfish search during repositioning movements; Li et al. 1985), binocular disparity (Wetterer 1989), and a combination of stimulus recognition (e.g., learned allometric relationships for morphology) and visual angle (Tegeder and Krause 1995). The ability of fish to estimate distance as travel time, or the inverse of encounter rate, is important in optimal foraging models where prey encounters are simultaneous (Stephens and Krebs 1986).

In situations where more than one prey is visible at a particular time, a progressive shift in prey preference to larger prey occurs as planktivorous bluegill grow (Fig. 3). Small bluegill (<17 mm SL) preferentially attack *Daphnia* similar in size to the smallest size-class used here (Fig. 3), but small bluegill will also attack *Daphnia* in the largest size-class when they are the only prey available (Walton et al. 1992). Larger

prey are incorporated into the diet as the fish grow and capture efficiency increases. Prey size preference shifts markedly for bluegill between 10 and 29 mm SL (Fig. 3). At 29 and 38 mm SL, bluegill can effectively capture prey in each size-class and attack *Daphnia* as encountered when prey density is between 9 and 20 individuals·L<sup>-1</sup>. Larger bluegill (i.e., >38 mm SL) exhibit preferences for the largest *Daphnia* size-class.

Our visual angle results suggest that small bluegill are significantly better at detecting their preferred small prey than they are at perceiving large prey; however, the difference between the MLDs to the smallest and largest prey is smaller than expected under the assumption of independence of visual angle on prey size. If visual angle is independent of prey size, then the MLD to the smallest prey should be approximately 34% of the MLD to the largest prey. On average, MLDs to the smallest prey were only about 70% of the MLDs to the largest prey. Reaction distances of small bluegill to prey of different sizes do not differ as much as do those of larger conspecifics for which visual angle is independent of prey size.

Poor visual and locomotory capabilities of small bluegill probably contribute to the comparatively small differences in reaction distances to small versus large prey. Bluegill exhibit saltatory search behavior where repositioning movements occur between locomotive pauses (Janssen 1982; Ehlinger and Wilson 1988; O'Brien et al. 1989). Prey selection occurs primarily during the pauses. The geometry of the search space and the movement patterns of fish utilizing a saltatory search strategy change with environmental conditions, prey type (O'Brien et al. 1989), and ontogeny (Browman and O'Brien 1992a, 1992b). Although visual resolution is initially poor, vision improves rapidly in young-of-the-year bluegill (Walton et al. 1994). The reaction distance and the distance over which attacks are carried out increase directly with fish size. Browman and O'Brien (1992a) found, however, that white crappie (*Pomoxis annularis*) larvae did not efficiently moderate the distance between locomotive pauses; the distance between pauses was longer than the location distance. Search behavior became more energetically efficient as fish grew. The swimming movements of large juveniles (>20 mm SL) are about 40% of the MLD and are directly related to prey size (O'Brien et al. 1989).

Several factors might lessen the distance over which a small bluegill will react and initiate an attack on prey. Small bluegill search comparatively small visual volumes, may require a minimum distance before initiating an attack because of poor attack ability, and may be learning to recognize prey. Further, attacks by small fish are more deliberate than those of larger juveniles, and the attack posture (i.e., sinuous posture) of larvae requires that the fish be located close to prey before initiating an attack (Browman and O'Brien 1992a). The variance around the mean reaction distance and the minimum reaction distance increased directly with bluegill size (Fig. 2).

Larval fish also often track the movement of individual prey (Browman and O'Brien 1992a), and while this may give the fish an indication of distance and (or) prey size, a small bluegill may not immediately exhibit the characteristic reaction behavior when it sees a prey. The fact that the minimum reaction distance increases directly as a function of fish size suggests that bluegill might be assessing prey location prior to the terminal pause before initiating an attack, perhaps at the

penultimate pause or during transits. That is, if a 31-mm bluegill were searching for prey only during pauses, then by chance alone one might expect the fish to pause within 11 cm of a prey. Yet, reaction distances <11 cm were not observed for 31-mm bluegill.

Are our findings biologically significant or merely a statistical error (i.e., a Type II error)? Use of the MLD reduces sample size and the power of the statistical comparisons. The power of the comparisons of MLDs to the largest prey versus the two other prey categories for bluegill >20 mm SL is >0.75. The power of similar comparisons for the mean reaction distance was >0.8 for all bluegill size categories. Comparisons of MLDs to small- versus medium-sized prey are generally less powerful (power <0.5) as are comparisons for the mean reaction distance (power ranged from 0.1 to 0.99). The statistical significance of the comparisons is opposite that expected from a reduction in sample size: the mean reaction distance to different-sized prey did not differ significantly within fish size categories for bluegill <25 mm SL whereas the MLDs to the largest versus smallest prey differed significantly. Even though the ratio of the mean reaction distance to the smallest versus largest prey is approximately 0.7 across the fish size-classes, the difference between reaction distances to each of the three prey size categories increases directly as fish grow (Table 1). Increasing sample size would aid in distinguishing among the mean reaction distances of bluegill <25 mm SL to the three prey size categories; however, the power of overall statistical comparison of visual angles (based on the MLD) among prey size categories is high, about 0.89.

We also assumed that each reaction distance measurement represents an independent observation. Pseudoreplication in behavior studies can underestimate *P*-values (Lombardi and Hurlbert 1996). However, if we assume a worst-case scenario where MLD measurements are based on only one fish per prey size category at each fish size-class ( $N = 26$ ), then visual angles are still significantly different among prey size-classes (ANCOVA of prey size on ln-transformed  $\theta$  using ln-transformed SL as the covariate; prey size:  $F_{2,22} = 26.58$ ,  $P < 0.0001$ ).

Visual angle is assumed to be independent of prey size and to provide a measure of either the visibility of the prey or the visual capability of the predator. Prey size and the changing visual capabilities of fishes during growth play significant roles in estimation of the encounter probabilities required for most diet choice and habitat switching models where the availability of prey in the environment is a function of visibility (Werner and Hall 1974; O'Brien et al. 1976; Mittelbach 1981; Eggers 1982; Askes and Giske 1990, 1993). Because the distribution of attacks on prey differs significantly from that expected from prey visibility alone, planktivorous bluegill presumably incorporate a decision rule before they react to prey (Walton et al. 1992). Prey selection by small bluegill is constrained by several factors. In addition to locomotive and visual constraints, mouth gape and digestibility of prey are thought to constrain prey selection by small planktivorous fish (Mills et al. 1984; Walton et al. 1992). Our results indicate that visual angles of small bluegill are not independent of prey size. Consequently, when the composition of the preferred diet differs from the prey that are most readily detected, visual angle may not measure prey visibility or the fish's visual capability. This result draws into question the interpretation of reaction

distance and visual angle studies, and their application to encounter rates, particularly for small fishes in nature. Prey size preferences and search behavior must be taken into account when using small fish and comparing behavioral measures of vision among species.

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## References

- Aksnes, D.L., and Giske, J. 1990. Habitat profitability in pelagic environments. *Mar. Ecol. Prog. Ser.* **64**: 209–215.
- Aksnes, D.L., and Giske, J. 1993. A theoretical model of aquatic visual feeding. *Ecol. Model.* **67**: 233–250.
- Baerends, G.P., Bennema, B.E., and Vogelzang, A.A. 1960. Über die Änderung der Sehschärfe mit dem Wachstum bei *Aequidens portalegrensis* (Hensel) (Pisces, Cichlidae). *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere*, **88**: 67–78.
- Beard, T.D. 1982. Population dynamics of young-of-the-year bluegill. *Wis. Dep. Nat. Resour. Tech. Bull. No.* 127.
- Blaxter, J.H.S. 1975. The eyes of larval fish. *In* Vision in fishes. Edited by M.A. Ali. Plenum Press, New York. pp. 427–443.
- Breck, J.E., and Gitter, M.J. 1983. Effect of fish size on the reaction distance of bluegill (*Lepomis macrochirus*). *Can. J. Fish. Aquat. Sci.* **40**: 162–167.
- Browman, H.I., and O'Brien, W.J. 1992a. The ontogeny of search behavior in the white crappie, *Pomoxis annularis*. *Environ. Biol. Fishes*, **34**: 181–195.
- Browman, H.I., and O'Brien, W.J. 1992b. Foraging and prey search behaviour of golden shiner (*Notemigonus crysoleucas*) larvae. *Can. J. Fish. Aquat. Sci.* **49**: 813–819.
- Browman, H.I., Gordon, W.C., Evans, B.I., and O'Brien, W.J. 1990. Correlation between histological and behavioral measures of visual acuity in a zooplanktivorous fish, the white crappie (*Pomoxis annularis*). *Brain Behav. Evol.* **35**: 85–97.
- Cameron, D.A., and Pugh, E.N., Jr. 1991. Double cones as a basis for a new type of polarizatism vision in vertebrates. *Nature (London)*, **353**: 161–164.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology*, **64**: 1297–1304.
- Easter, S.S., Jr. 1992. Retinal growth in foveated teleosts: nasotemporal asymmetry keeps the fovea in temporal retina. *J. Neurosci.* **12**: 2381–2392.
- Eggers, D.M. 1982. Planktivore preference by prey size. *Ecology*, **63**: 381–390.
- Ehlinger, T.J., and Wilson, D.S. 1988. Complex foraging polymorphism in bluegill sunfish. *Proc. Natl. Acad. Sci. U.S.A.* **85**: 1878–1882.
- Ewert, J.-P., and Burghagen, H. 1979. Ontogenetic aspects on visual 'size-constancy' phenomena in the midwife toad *Alytes obstetricans* (Laur.). *Brain Behav. Evol.* **16**: 99–112.
- Ewert, J.-P., and Gebauer, L. 1973. Grössenkonstanzphänomene im Beutefangverhalten der Erdkröte (*Bufo bufo* L.). *J. Comp. Physiol.* **85**: 303–315.
- Fernald, R.D. 1988. Aquatic adaptations in fish eyes. *In* Sensory biology of aquatic animals. Edited by J. Atema, R.R. Fay, A.N.

- Popper, and W.N. Tavolga. Springer-Verlag, New York. pp. 435–466.
- Guthrie, D.M., and Muntz, W.R.A. 1993. Role of vision in fish behaviour. *In* Behaviour of teleost fishes. 2nd ed. *Edited by* T.J. Pitcher. Chapman and Hall, London, U.K. pp. 89–128.
- Hairston, N.G., Jr., Li, K.T., and Easter, S.S., Jr. 1982. Fish vision and the detection of planktonic prey. *Science* (Washington, D.C.), **218**: 1240–1242.
- Hughes, R.H. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. *Am. Nat.* **113**: 209–221.
- Ingle, D. 1968. Visual releasers of prey-catching behavior in frogs and toads. *Brain Behav. Evol.* **1**: 500–518.
- Janssen, J. 1982. Comparison of the searching behavior for zooplankton in an obligate planktivore, blueback herring (*Alosa aestivalis*) and a facultative planktivore, bluegill (*Lepomis macrochirus*). *Can. J. Fish. Aquat. Sci.* **39**: 1649–1654.
- Johns, P.R., and Easter, S.S., Jr. 1977. Growth of the adult goldfish eye. II. Increase in retinal cell number. *J. Comp. Neurol.* **176**: 331–342.
- Li, K.T., Wetterer, J.K., and Hairston, N.G., Jr. 1985. Fish size, visual resolution, and prey selectivity. *Ecology*, **66**: 1729–1735.
- Lombardi, C.M., and Hurlbert, S.H. 1996. Sunfish cognition and pseudoreplication. *Anim. Behav.* **52**: 419–422.
- McFarland, D. 1985. *Animal behavior*. Benjamin/Cummings Publishing Co., Menlo Park, Calif.
- Meyer, A. 1986. Changes in behavior with increasing experience with a novel prey of the Central American cichlid, *Cichlasoma managuense* (Teleostei: Cichlidae). *Behaviour*, **98**: 145–167.
- Mills, E.L., Confer, J.L., and Ready, R.C. 1984. Prey selection by young yellow perch: the influence of capture success, visual acuity, and prey choice. *Trans. Am. Fish Soc.* **113**: 579–587.
- Mittelbach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology*, **62**: 1370–1386.
- Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology*, **65**: 499–513.
- Müller, H. 1952. Bau und Wachstum der Netzhaut des Guppy (*Lebistes reticulatus*). *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere*, **63**: 275–324.
- O'Brien, W.J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. *Am. Sci.* **67**: 572–581.
- O'Brien, W.J., and Evans, B.I. 1991. Saltatory search behavior in five species of planktivorous fish. *Verh. Int. Ver. Theor. Angew. Limnol.* **24**: 2371–2376.
- O'Brien, W.J., Slade, N.A., and Vinyard, G.L. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). *Ecology*, **57**: 1304–1310.
- O'Brien, W.J., Evans, B.I., and Browman, H.I. 1989. Flexible search tactics and efficient foraging in saltatory searching animals. *Oecologia*, **80**: 100–110.
- O'Brien, W.J., Browman, H.I., and Evans, B.I. 1990. Search strategies of foraging animals. *Am. Sci.* **78**: 152–160.
- Otten, E. 1981. Vision during growth of a generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae). *Neth. J. Zool.* **31**: 650–700.
- Sivak, J.G. 1990. Optical variability of the fish lens. *In* The visual system of fish. *Edited by* R.H. Douglas and M.A.B. Djamgoz. Chapman and Hall, London, U.K. pp. 63–80.
- Stephens, D.W., and Krebs, J.R. 1986. *Foraging theory*. Princeton University Press, Princeton, N.J.
- Tegeeder, R.W., and Krause, J. 1995. Density dependence and numerosity in fright stimulated aggregation behaviour of shoaling fish. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **350**: 381–390.
- van der Meer, H.J., and Anker, G.C. 1984. Retinal resolving power and sensitivity of the photopic system in seven haplochromine species (Teleostei, Cichlidae). *Neth. J. Zool.* **34**: 197–209.
- Vinyard, G.L., and O'Brien, W.J. 1976. Effects of light and turbidity on the reactive distance of bluegill sunfish (*Lepomis macrochirus*). *J. Fish. Res. Board Can.* **33**: 2845–2849.
- Wagner, H.-J. 1978. Cell types and connectivity patterns in mosaic retinas. *Adv. Anat. Embryol. Cell Biol.* **55**: 1–81.
- Wahl, C.M., Mills, E.L., McFarland, W.N., and DeGisi, J.S. 1993. Ontogenetic changes in prey selection and visual acuity of the yellow perch, *Perca flavescens*. *Can. J. Fish. Aquat. Sci.* **50**: 743–749.
- Walton, W.E., Hairston, N.G., Jr., and Wetterer, J.K. 1992. Growth-related constraints on diet selection by sunfish. *Ecology*, **73**: 429–437.
- Walton, W.E., Easter, S.S., Jr., Malinoski, C., and Hairston, N.G., Jr. 1994. Size-related change in the visual resolution of sunfish (*Lepomis* spp.) *Can. J. Fish. Aquat. Sci.* **51**: 2017–2026.
- Wanzenböck, J. 1992. Ontogeny of prey attack behaviour in larvae and juveniles of three European cyprinids. *Environ. Biol. Fishes*, **33**: 23–32.
- Wanzenböck, J., and Schiemer, F. 1989. Prey detection in cyprinids during early development. *Can. J. Fish. Aquat. Sci.* **46**: 995–1001.
- Werner, E.E., and Hall, D.J. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology*, **55**: 1042–1052.
- Werner, E.E., and Hall, D.J. 1988. Ontogenetic habitat shifts in the bluegill: the foraging rate – predation risk tradeoff. *Ecology*, **69**: 1352–1366.
- Wetterer, J.K. 1989. Mechanisms of prey choice by planktivorous fish: perceptual constraints and rules of thumb. *Anim. Behav.* **37**: 955–967.
- Wetterer, J.K., and Bishop, C.J. 1985. Planktivorous prey selection: reactive field volume model versus the apparent size model. *Ecology*, **66**: 457–464.