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Growth of the teleost eye: novel solutions to complex constraints

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Synopsis

The cichlid fish, *Haplochromis burtoni*, is highly dependent on vision for survival in its natural habitat. As is true of most teleost fishes, the eyes continue to grow throughout life without any obvious changes in visual capability. In *H. burtoni*, for example, retinal area may increase by 27× in just 6 months. During growth, there is no obvious change in the visual sensitivity, visual acuity or lens quality which must all be appropriate for the enlarging eye. This requires that during growth competing constraints be met. For example, to maintain visual acuity, the number of ganglion cells per visual angle subtended on the retina must remain the same as must the convergence ratio of the cones onto those ganglion cells. In contrast, to maintain visual sensitivity, the number of rod photoreceptors per unit retinal area must remain the same. These requirements are in conflict since a larger eye may preserve acuity with fewer cells per unit area in a larger retina. In addition, the lens properties must remain the same as the animal increases in size so that the image available is of similar quality throughout life. Experiments have been performed to reveal the adaptations during growth which allow the fish to preserve its image of the world throughout life.

Introduction

The African cichlid fish, *Haplochromis burtoni*, relies primarily on visual recognition of particular chromatic and spatial patterns to mediate important social interactions. In its natural habitat, the shore pools of Lake Tanganyika, males defend territories from which they court females (Fernald & Hirata 1977a, b). A female, after spawning in a male's territory, broods the developing young in her mouth for approximately 12–14 days, well away from the territory. The overall area of the territorial arena is limited by suitable substratum, and the total number of territories is determined by male-male competition (Fernald & Hirata 1977b).

Adult males have distinctive color patterns which are important both for the maintenance of territories and for reproductive behavior. These patterns are: black forehead stripes, black opercular spot and eye-bar, blue or yellow body color, yellow-orange egg spots on the anal fin, black pelvic fins, orange humeral scales and blue lips (Fig. 1). Non-territorial males remain in a school together outside the territorial arena with females and juveniles. The animals live in turbid shore pools in which measurements of transmissivity revealed that light in the blue and orange regions of the spectrum are transmitted significantly better than at other wavelengths (Fernald & Hirata 1977a). These color regions are well matched to the chromatic patterns used for social signalling (Fernald 1977).

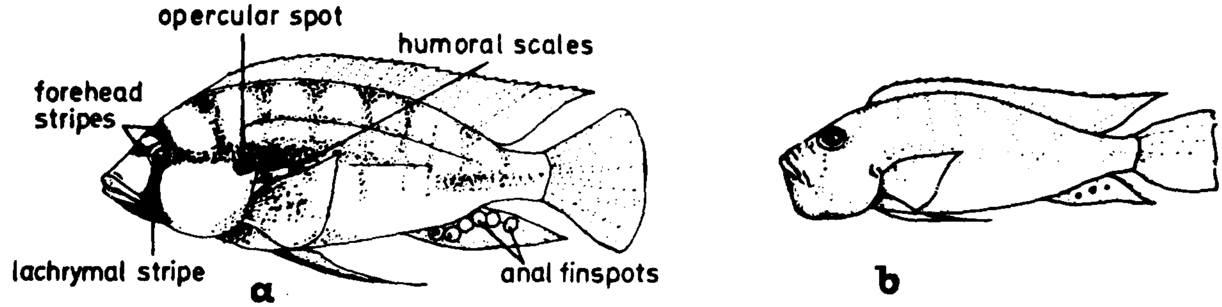

Fig. 1. Schematic illustration of the coloration patterns of a territorial adult male (a) and an adult female (b) *Haplochromis burtoni*. The lachrymal stripe (eye to mouth bar), forehead stripes and opercular spot of adult males are black. The humoral scales are orange-red and the 5 to 9 anal fin spots are yellow-orange. The dorsal and caudal fins have rows of small reddish spots between the rays; pectoral fins are transparent and the pelvic fins have a black lower edge. The female is shown with young in her buccal cavity. Females are cryptically sandy colored except for a few small anal fins spots which are pale yellow-orange.

Since vision is so important for behavior in this species, it is not surprising to realize that the eye enlarges enormously as the animal grows. Since most teleosts continue to grow throughout life, the relative rate of eye growth generally depends on the overall rate of growth and on the allometric relationship between body size and eye size. In other cases studied (goldfish, Johns 1977, guppy, Müller 1952), the size changes significantly more slowly than in *H. burtoni*, where the radius of the eye may triple during the first two months of life. The growth and developmental rate are strongly influenced by the social situation (Fernald & Hirata 1980, Fraley & Fernald 1982). Specifically, males which grow up defending territories grow and mature much faster than do broodmates which grow up without territories (Fraley & Fernald 1982). This slowing of the growth and maturation is reflected in the time onset of coloration patterns, the onset of behavior patterns, rate of whole body growth and rate of testicular development. From analysis of these measures, it is clear that non-territorial males are not prevented from maturing, but that both the rate and phenotypic expression of maturation are inhibited in these males. Although those studies were done within groups of broodmates, our more recent observations suggest that these effects are even more pronounced if there is a size difference between territorial and non-territorial animals (Muske & Fernald, unpublished). Such regulation of development may be adaptive in a social system where territorial space is limited.

In the shore pools where *H. burtoni* live, only about 10% of the adult males are able to breed (Fernald & Hirata 1977b). These breeding males are brightly colored, highly visible and much more likely to be preyed upon. When one such territorial animal is removed by a predator, the non-territorial males quickly congregate and fight over the space, with the winner acquiring not only the territory, but the concomitant territorial coloration and behavioral patterns. Despite the fact the siblings may have eyes differing in size by a factor of two in a period of just four months, there is no obvious difference in their visual abilities.

To preserve visual function during this growth, three critical features of the functioning eye must be conserved: (1) the photopic visual acuity; (2) the scotopic visual sensitivity; and (3) the optimal quality of the lens. Maintaining these essential properties of the eye imposes apparently conflicting constraints on the growth of the eye. Here I will first describe the retinal structure in *H. burtoni*, then the process of retinal growth and finally, I will outline our current understanding of the novel solutions to each of the problems posed by such postnatal growth.

Retinal structure and growth

Teleosts have a retinal structure characteristic of all vertebrates with well defined, alternating layers of neuropil and cell bodies arranged in a transparent