

The evolution of complex brains and behaviors in African cichlid fishes

Caroly A. Shumway^{1,2**}

¹ Boston University, Department of Biology, 5 Cummington Street, Boston, MA, USA, 02215

² Brown University, Department of Psychology, Hunter Lab, 89 Waterman Street, Providence, RI, 02912, USA

Abstract In this review, I explore the effects of both social organization and the physical environment, specifically habitat complexity, on the brains and behavior of highly visual African cichlid fishes, drawing on examples from primates and birds where appropriate. In closely related fishes from the monophyletic Ectodini clade of Lake Tanganyika, both forces influence cichlid brains and behavior. Considering social influences first, visual acuity differs with respect to social organization (monogamy versus polygyny). Both the telencephalon and amygdalar homologue, area Dm, are larger in monogamous species. Monogamous species are found to have more vasotocin-immunoreactive cells in the preoptic area of the brain. Habitat complexity also influences brain and behavior in these fishes. Total brain size, telencephalic and cerebellar size are positively correlated with habitat complexity. Visual acuity and spatial memory are enhanced in cichlids living in more complex environments. However habitat complexity and social forces affect cichlid brains differently. Taken together, our field data and plasticity data suggest that some of the species-specific neural effects of habitat complexity could be the consequence of the corresponding social correlates. Environmental forces, however, exert a broader effect on brain structures than social ones do, suggesting allometric expansion of the brain structures in concert with brain size and/or co-evolution of these structures [*Current Zoology* 56 (1): 144–156 2010].

Key words Fish, Evolution, Brain, Behavior, Social organization, Habitat complexity

What causes a complex brain? Complex brains and behaviors have arisen throughout vertebrate evolution, in all vertebrate classes. In recent years, progress in understanding the evolution of brains and behaviors has been made possible through quantification of complexity, increased use of phylogenetically sound comparisons, and experimental manipulations and hypothesis testing (Pollen and Hofmann, 2008; Shumway, 2008). We now know that changes in brain structure likely reflect a combination of developmental forces, adaptation, and drift (Striedter, 2005).

My long-term goal is to understand the relationship between complex behaviors and complex brains and the forces underlying such change. My collaborators and I seek to understand how complex brains and behaviors are shaped over developmental and evolutionary time, using closely related African cichlid fishes. Due to the fine ecological, behavioral, and neuronal comparisons that can be made, African cichlids provide an unparalleled opportunity to understand how environmental and social pressures influence neural evolution. They live in habitats of varying structural complexity ranging from

sand to large fusiform rocks, exhibit diverse feeding strategies ranging from detritivores to scale-eaters, and differ in social behaviors ranging from polygyny to monogamy; however, they share close genetic similarity. Cichlids are highly visual, and their visual behavior is well studied (cf., Fernald, 1982; Carleton and Kocher, 2001).

My research subjects are the clade Ectodini in Lake Tanganyika, which comprises 35 species. The species differ in both habitat preference and social organization (Barlow, 2000). The number of species coupled with the behavioral diversity present within the clade enables judicious selection of species varying either in abiotic habitat preference (sand/intermediate habitats/rock) or in social type (monogamy/polygyny) while keeping feeding behavior constant (Konings, 1996; Konings and Dieckhoff, 1992). Relative telencephalic volume can vary as much as two-fold among species in this clade (personal observations). Recent consensus phylogenies suggest that sand dwelling is the ancestral trait and that rock dwelling independently evolved twice in the clade (Fig. 1; also see Koblmüller et al., 2004). There are also

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* Corresponding author. E-mail: caroly.shumway@gmail.com. Current address: 76 Great Road, North Smithfield, RI 02896, USA.

Phone: 401-769-3659; Fax: 401-769-4598.

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at least four independent transitions between monogamy and polygyny in the evolutionary history of the clade (Fig. 1; Koblmüller et al., 2004).

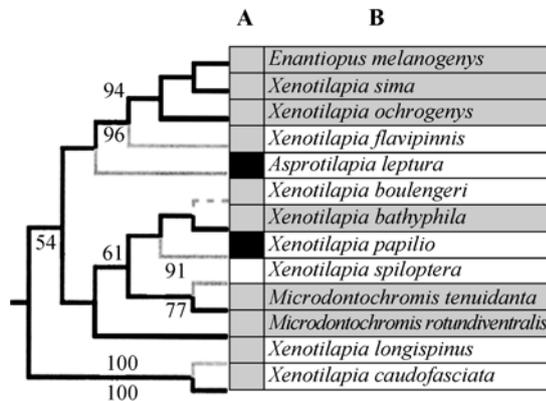


Fig. 1. Mapping of character traits onto the phylogeny of the clade Ectodini

A. (Squares) Habitat preference: sand dwelling (gray squares); intermediate (white); rock dwelling (black).

B. (Rectangles) Social organization: monogamy (white rectangles); polygyny (gray). Phylogeny based on Koblmüller, 2004.

Understanding which forces are most important in telencephalic expansion – social, environmental, or both – is of great importance in not just teleost evolution, but in primate and bird evolution as well (Bshary et al., 2002; Dunbar and Shulz, 2007; Lefebvre and Sol, 2008). These species groups share a number of similarities. They exhibit a considerable range of brain to body weight ratios within their groups. The size of higher-order brain regions varies among species (Bullock, 2002). Often highly visual, these species inhabit a variety of habitat types, exhibit a range of social systems, and differ in cognitive abilities. Due to their indeterminate growth, however, fishes are thought to be freer from developmental constraints on brain expansion than other vertebrates are (Kotsrschal et al., 1998). In most fishes, skull volume is considered unlikely to be a constraint on brain size, since the brain is considerably smaller than the skull cavity. Brain size may be constrained only in the smallest fish; the smaller the fish, the proportionately larger its brain. The reduced developmental constraints, the whole-genome duplication that occurred twice in the teleost lineage (Ohno, 1970; Amores et al., 1998), and the tremendous diversity of fish habitats leading to differential selective pressures may explain the extraordinary diversity of fish brains and behaviors that exist today.

Given the intricacy of the neural substrates underlying complex behaviors, comparative studies of closely related species can be a particularly powerful approach

(e.g., Healy et al., 2005; Lefebvre and Sol, 2008). In this review, I present my laboratory's preliminary and published results showing how social organization and habitat complexity, respectively, shape brain structure and function in Tanganyikan cichlids of the Ectodini clade (Dobberfuhl et al., 2005; Scace et al., 2006; Pollen et al., 2007; Shumway et al., 2007; Shumway, 2008).

1 Materials and Methods

Here I provide a brief description of each technique that my colleagues and I have used to compare the different social conditions and levels of habitat complexities in Lake Tanganyika in order to examine the effects on visual processing, the size of the brain and its structures, and hormones and behavior among cichlid species.

1.1 Quantifying habitat complexity

Shumway et al. (2007) measured benthic rugosity from 25-m² quadrats to compare habitat complexity among the different benthic environments in Lake Tanganyika. The rugosity value was determined as the ratio of the chain length to rope length, normalized by calculating a Z score (Zar, 1999). Intensity analysis is a purely visual, scale-independent measure of habitat differences. Essentially, the method is a measure of the variation in optical intensity obtained from video images of a quadrat. Each quadrat was assigned to one of three qualitative categories: “sand”, “intermediate”, or “rock”, based on the presence or absence of sand and large rocks. “Intermediate” signified mixed habitat, such as sand with small- to medium-sized rocks or sand with grasses. Five randomly selected frames from each quadrat were grabbed from the video using Digital Origin's MotoDV (Version 1.4), copied into either Adobe PhotoShop (Version 8.0) or GIMP (GNU Image Manipulation Program, and imported into Image Pro Plus (Version 3.0) to produce a grayscale bitmap analysis of each image. Subsequent intensity analysis of the bitmap produced intensity values for each pixel in the image. The standard deviation of the intensity values was determined for each of the five images, and the mean of the standard deviations was determined for the group of five images per quadrat. The normalized mean standard deviation was used for statistical comparison among quadrats.

1.2 Visual acuity

Dobberfuhl et al. (2005) compared visual behavior between species (*Asprotilapia leptura*, *Xenotilapia spiloptera*, *Xenotilapia flavipinnis* and *Enantiopus melanogenys*) differing either in habitat preference or

social organization by measuring mean visual acuity. A fish was placed in a circular drum. The visual stimulus was a square-wave stimulus consisting of black and white stripes of equal width on the internal side of the drum. The stimulus completely filled the fish's visual field. Eight different grating cycles as well as a gray grating (50% gray) were used. Each stimulus was rotated 4 rpm by a variable-speed reversible DC motor. Visual acuity of the fish was determined from both optomotor and optokinetic responses. A positive response consisted of a combination of smooth tracking eye movements followed by reset saccades and/or locomotory following of the moving stripes.

1.3 Neuroanatomical measures

1.3.1 Telencephalon To determine which telencephalic structure(s) contributed to the observed telencephalic expansion in monogamous species, brains of both monogamous and polygynous males were sectioned at 50 μ m on a cryostat. Volumetric measures of telencephalic regions were obtained with Image Pro image analysis software.

1.3.2 AVT measures The level of vasotocin in the preoptic area between the monogamous and polygynous males was compared by using the primary R82 AVT antibody (1:4000), which labels AVT in fish. Perfused brains (4% paraformaldehyde) were stored in fix for 12 hrs at 4°C, cryoprotected, embedded in OCT, frozen at -60°C, cut at 20 μ m on a cryostat, dried, and rinsed for 15 min in PBS. Endogenous peroxidase was quenched in a 0.3% H₂O₂ methanol solution for 20 min and rinsed in H₂O for 2 min and in PBS for 5 min. To prevent non-specific tissue staining, sections were incubated with blocking solution (10 ml 1 \times PBS, 0.25 g BSA, 100 μ l 30% Triton-X) for 1 h at room temperature in a humid chamber. After an 18-hr incubation at 4°C with primary antibody, the antibody was removed by 3 \times 5-min rinses in 1 \times PBS. Sections were incubated for 30 min with a biotinylated secondary antibody solution, followed by 30 min in ABC solution (Vector Labs). The antibody was visualized with a diaminobenzidine (DAB) solution and counterstained.

1.3.3 Brain structure size To compare the size of the brain and relevant brain structures among 7 focal species, volumes were determined from photographs of the whole brain (Pollen et al., 2007). The brain stem and nerves were trimmed from the brains, and the brain mass was recorded. Photographs of perfused whole brains were taken with a Zeiss dissecting microscope using a digital camera and Zeiss Axiovision mrc software. The volume (V) of brain structures was deter-

mined according to an ellipsoid model $V = (L \times W \times H)\pi/6$. For paired structures such as the telencephalon, the estimated volume of the structure was doubled. We controlled for phylogeny with independent contrasts using CAIC.

1.4 Spatial learning

To compare spatial learning between rock- and sand-dwelling species, individual *X. flavipinnis* and *A. leptura* were tested in a sequential rectangular maze containing three inner walls. Each wall contained two open doors. The correct door was marked with a yellow circle, a local landmark. A fourth wall, also with two doors, led to the end, which was signified by a yellow triangle on the rear wall. Dead ends, which represented incorrect choices, were unmarked. Two extramaze cues, a large circle and star, were provided outside the maze. *Acclimation*: The fish was initially allowed to explore the sequential maze with no cues present for 30 min. Subsequent acclimation periods lasted 20 min. *Pre-training* (visual plus food cues): The fish was rewarded with food at each of the three local landmarks (yellow circles) and at the end (yellow triangle). Dead ends were placed at the incorrect door choices. The fish had to successfully complete three pre-training trials to move to the next phase. *Training* comprised both visual cues plus a food cue at the end. The fish had to successfully complete two training trials. *Test* trials included visual cues only. Trials were run until the fish either completed the task to criterion (two wrong turns per test) or completed 18 trials. The position of the local landmarks was randomly determined for each pair of animals tested, one from each species. Both the time to completion and the number of wrong turns were recorded.

1.5 Plasticity

The role of plasticity underlying the observed social and environmental differences among species was explored using lab-reared *X. flavipinnis* fry that were kept in 5-gal tanks under temperature, light, and pH conditions similar to those of their natural environment. To avoid any external stimuli, the walls of the tanks were covered in opaque wrapping, and the filters and heaters were kept behind a divider. The fry were separated into three groups. The environmental treatment group was placed as a group into a tank with a rocky substrate, which represented enriched habitat complexity and normal social complexity. Isolated individuals in the social treatment group were placed in sandy tanks of the same size as the controls, which represented normal habitat complexity and impoverished social com-

plexity. The control group was placed into a tank with a sandy substrate, which represented normal habitat and social complexity. Visual acuity was measured at 4 and 12 months. To control for differences in lens size, visual acuity was measured in the experimental groups when their body lengths were statistically indistinguishable from those of the controls.

2 Results

2.1 Quantifying complexity

Quantification of complexity is essential in the search for factors underlying speciation and the development of behavioral and neural complexity. Without quantification and the use of a continuous variable, it is impossible to discern whether there are corresponding quantitative or qualitative shifts in brain and behavior as an animal evolves in a new environment.

A number of habitat complexity measures have been developed (e.g., Risk, 1972; Wilkens and Myers, 1992; McCormick, 1994; Sanson et al., 1995; Caley and St. John, 1996; Garcia-Charton and Pérez-Ruzafa, 2001). Shumway et al. (2007) used two measures to quantify habitat complexity in Lake Tanganyika: rugosity, or surface topography, a standard measure used in coral reef biology (Risk, 1972; Luckhurst and Luckhurst, 1978), and a new video-based technique we developed called optical intensity (see Section 2.1 for methods). Optical intensity is a scale-independent visual technique that measures the variation in optical intensity obtained from video images (Shumway et al., 2007). We tested the technique on 38 quadrats in Lake Tanganyika to determine if three freshwater habitats (sand, intermediate, and rock) were quantitatively different. The method revealed significant differences among these habitats. The measures of rugosity and optical intensity were positively correlated. Combining both continuous measures may ensure a more robust analysis (McCormick, 1994), as each variable is influenced by different aspects of the surface topography.

It is much more difficult to quantify social complexity. Should a unitary measure be obtained, and is this valid for comparison across species? The problem is that researchers have not agreed on the best social measure, nor is it clear how universally applicable such a test could be. In captive primates, Deaner et al. (2006) showed that a number of cognitive measures co-varied in primates. They suggested that these reflected a domain general intelligence, known as “g” in psychology. However, brain-behavior comparisons can vary depending on the brain structure being tested and the way

in which it is measured. Deaner et al. (2007) showed, for example, that general intelligence correlated best with absolute brain size, but not with brain size residuals (Deaner et al., 2007). In wild primates, brain size correlated with group size, range, and home range (Sawaguchi, 1988), but neocortex size correlated only with group size (Dunbar, 2002). In our research, we have compared relative brain size and size of brain structures with species richness, number of individuals, and type of social organization among the Ectodini species (Pollen et al., 2007). We found differences for all measures. We have also compared aggressive and affiliative behaviors between monogamous and polygynous species and found significant differences (Shumway and Hofmann, in prep). Another approach, originating from social anthropologists, is to compare groups of social traits across populations or species (Carneiro, 2000, 2003; A. Riveras, personal communication) using a Guttman scalogram (Guttman, 1950). This type of unidimensional analysis incorporates both the number and frequency of social traits; more complex groups exhibit more traits. The advantage of such an approach is that the traits can be tailored to fit particular species, families, or classes. Recent work has produced a multidimensional variation of Guttman scaling (Dancer, 2008) as well as cluster analysis of cultural complexity (Maxwell et al., 2002).

2.2 Information processing in the social brain

What are the neural and behavioral differences among cichlid species differing in social organization? One perplexing aspect of these sand-dwelling ectodine species is how similar their social environment is in the early phases of life. From fry to 12 months old (adult), both the monogamous and polygynous species school. They also share the same physical environment, occupying the same sand habitat and experiencing the same light levels and water quality, and have similar predators and heterospecifics (Konings, 1996; Shumway et al., unpublished data). Yet when the fish reach roughly 12 months of age, their social behavior diverges, with the polygynous species lekking during reproductive season and schooling at other times, and the monogamous species traveling in pairs.

To compare monogamous and polygynous Ectodini species, my collaborators and I used three approaches that have been useful in understanding the “social brain” in other systems: comparing differences in behavior among species exhibiting different types of social organization (described in Section 2.3), exploring the relationship between social complexity and brain structure

size (Section 2.4), and exploring the role of neuropeptides in social behavior (Section 2.5). To eliminate the confounding factor of habitat, we compared only sand-dwelling species, all benthic detritivores.

2.3 Visual processing and behavior

The social behavior of cichlid fishes relies upon the perception of visual signals that contain social significance; several species can recognize conspecifics by visual cues alone (e.g., Jordan et al., 2003). Different types of social organization, then, might affect visual processing and visually mediated behavior. How might the visual system differ between the two types of organization?

We found that social organization is associated with differences in visual acuity (Dobberfuhr et al., 2005). We compared the visual acuity of adults from two closely related species differing solely in social organization, or monogamy versus polygyny. The polygynous species *E. melanogenys* had better visual acuity (Fig.

2A). They detected spatial frequencies more than two times greater than the monogamous one did (*X. flavipinnis*, $P = 0.0002$) and a minimal separable angle (MSA) one-half the size (Fig. 2A; $P < 0.05$) (Dobberfuhr et al., 2005). We hypothesize that lekking, polygynous individuals may need to make more rapid choices based on various social cues, necessitating enhanced visual acuity. Upon encountering another individual, a male fish hovering over its sand crater needs to immediately determine if the other individual is a female or competitor male. In pilot field experiments, we counted the number of behavioral actions per minute during lekking for both a polygynous species and a reproductively active monogamous species ($n = 2$ species of each type). We found that polygynous animals exhibited two times more discrete behaviors per minute and interacted with five times more conspecifics per minute than did monogamous species (Fig. 2C, D; $P < 0.001$).

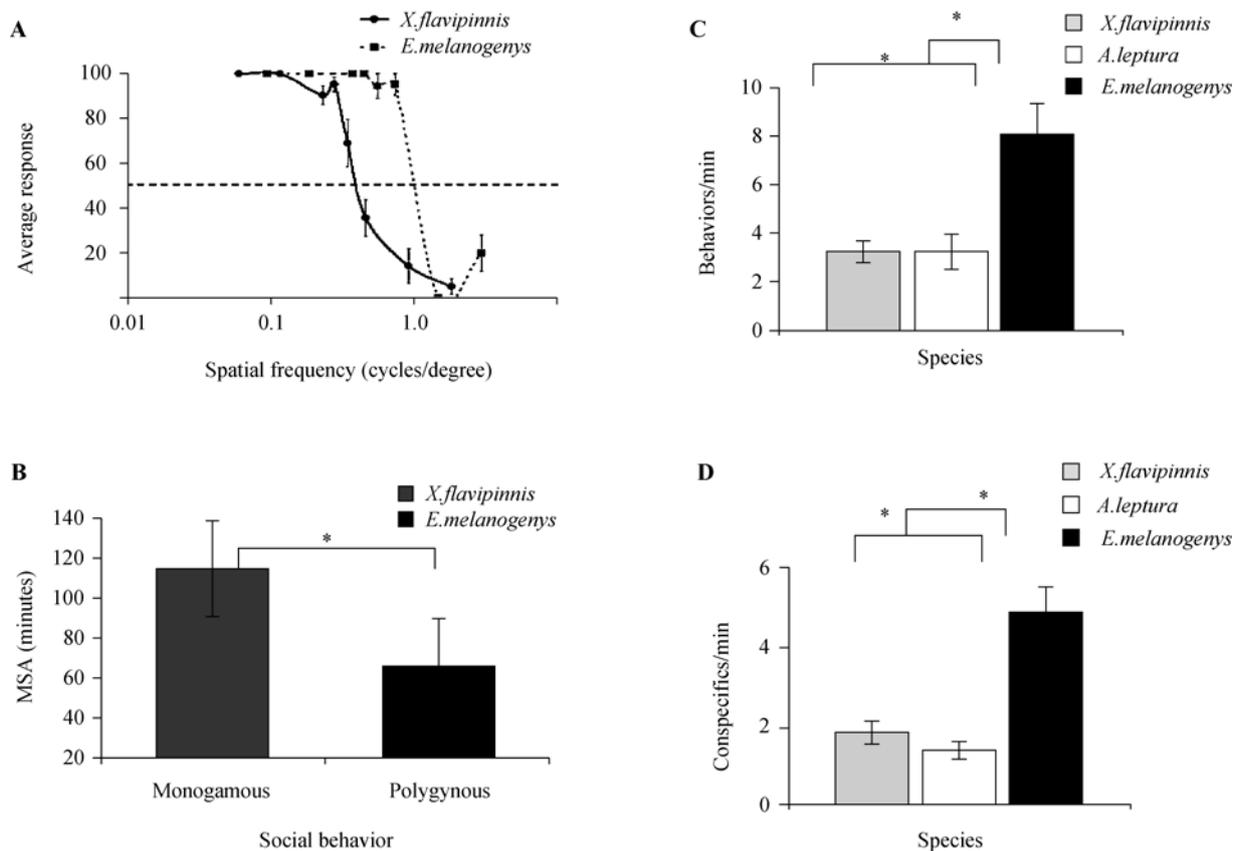


Fig. 2 Social organization and behavior

A, B. Visual acuity comparison between monogamous and polygynous species. **A.** Comparison of the average visual response at each spatial frequency. Error bars represent standard error. The dashed line represents the 50% response level; at this level, the polygynous, lek-forming *E. melanogenys* perceives a significantly higher spatial frequency than does the monogamous *X. flavipinnis* ($n = 7, 14$ respectively); $P < 0.05$). **B.** Mean minimum separable angle perceived by the two species. From Dobberfuhr et al., 2005, with permission. C, D. Comparison of the number of behavioral interactions in the field between monogamous and polygynous species. **C.** Number of behavioral interactions/minute in the field. **D.** Number of conspecific interactions/minute in the field. Light gray bar: monogamous *X. flavipinnis*; dark gray bar: monogamous *A. leptura*; black bar: the polygynous *E. melanogenys*.

2.4 Social organization and higher-order brain structures

A theoretical model of the social brain by Insel and Fernald (2004) suggests that, after unimodal sensory processing, higher-order centers such as the telencephalon and amygdala imbue social stimuli with meaning. Both structures play a role in social behavior. In vertebrates, telencephalic size has been correlated with social complexity, social learning, enhanced visual cognition, and innovation (Reader and Laland, 2002; Burish et al., 2004; but see Beauchamp and Fernandez-Juricic, 2004 for an opposing view). In fish, the telencephalon is known to be involved in a variety of social and cognitive behaviors, including courtship, parenting, and learning (Demski and Beaver, 2001). In 2007, we reported the finding that the telencephala of monogamous species were 15%–20% larger than those of polygynous species (Pollen et al., 2007), suggesting enhanced cognitive needs in monogamous species. Dunbar and Shultz (2007) subsequently demonstrated the same enlarged telencephala in monogamous birds and a variety of mammalian species, including bats, carnivores, and artiodactyls (e.g., cattle, deer, camels, hippopotamuses, sheep, and goats).

To determine which telencephalic structure(s) contributed to the telencephalic expansion observed in monogamous species, we obtained volumetric measures of telencephalic regions with image analysis software. In mammals, the amygdala has been implicated in both pair-bond formation and social recognition (Ferguson et al., 2001; Curtis and Wang, 2003). In fish, area Dm, the dorso-medial area of the telencephalon is believed to be the amygdalar homologue (Northcutt, 2006). In pilot experiments, we found that area Dm was 9.4% larger in the monogamous, pair-bonding *X. flavipinnis* than in the polygynous *X. ochrogenys* ($P = 0.04$, $n = 3$ fish per species, normalized for total brain volume). These results suggest that the task of social recognition required in pair-bonding monogamous animals may be driving amygdalar expansion.

2.5 Social organization and hormonal differences

In mammals, both the amygdala and the integrative area called the preoptic area (POA) are implicated in pair-bond formation (Curtis and Wang, 2003). In all vertebrates, the POA receives multimodal sensory information and may regulate telencephalic activity. It contains diverse neuropeptides, including arginine vasotocin (AVT) and the mammalian homologue arginine vasopressin (AVP). This family of neuropeptide hor-

mones is implicated in diverse complex social behaviors, including affiliative behavior (parental care, pair bonding, social recognition), aggression, fear behavior, and reproduction (Carter, 2002; Young and Wang, 2004). Variations in the AVP/AVT system may contribute to both interspecific and intraspecific variation in social behavior (Insel and Young, 2001; Insel and Fernald, 2004). AVP mediates social recognition: transgenic V1a knockout mice cannot recognize familiar conspecifics (Bielsky et al., 2004). While a role for AVT in pair bonding or mate choice in fishes has not been demonstrated, expression levels of AVT mRNA and the abundance of AVT mRNA-producing cells correlate with mating behaviors (Perry and Grober, 2003). AVT injections also inhibit social approach in highly social, but not in asocial, goldfish (Thompson and Walton, 2004).

We sectioned the brains of monogamous *X. flavipinnis* and polygynous *X. ochrogenys* and stained them with an AVT antibody. An observer blind to species type compared the number of AVT-ir cells in the POA and found that there were significant differences in the number of AVT-ir cells in the POA with respect to mating system. Corrected for body size (Miranda et al., 2003), monogamous male *X. flavipinnis* had over two times more AVT-ir cells than polygynous male *X. ochrogenys* ($P < 0.05$; $n = 4$ fish per species). These results, which corroborate differences in the AVT system between monogamous and polygynous voles (Insel and Fernald, 2004), support the notion that the AVT/AVP pathway is fundamental to vertebrate affiliation.

2.6 Complex habitats have social consequences

Complex habitats are important to many fish. Juvenile survival (e.g., Johnson, 2007), predation and predator avoidance strategies (Brown and Warburton, 1997), alternative male reproductive strategies (Lukasik et al., 2006), and home range size (Imre et al., 2002) are all correlated with habitat complexity. A spatially complex habitat, such as a coral reef or rock habitat, also provides more niche space than a simple one does (Caley and St. John, 1996). Thus, complex habitats have social consequences. Researchers have shown that social complexity, as measured by species richness, diversity, or abundance, has been correlated with habitat complexity. The causal role of complex habitats has been demonstrated experimentally for both species diversity and richness in fishes (Lingo and Szedlmayer, 2006). Shumway et al. (2007) compared the relationship between habitat complexity and social variables among the Ectodini clade in Lake Tanganyika, as measured by

rugosity, or surface topography, and our new video-based measure, optical intensity. Both complexity measures were directly correlated with species richness and diversity; optical intensity alone correlated with abundance. A similar correlation between habitat complexity and species diversity has previously been shown for intertidal rock pool fishes (Griffiths et al., 2006) and coral reef fishes (Luckhurst and Luckhurst, 1978). However, on coral reefs, correlations between abundance and complexity measures depend on the fish family, fish size, and location (Risk, 1972; Luckhurst and Luckhurst, 1978; Roberts and Ormond, 1987).

2.7 Complex habitats and visual processing

In the clade Ectodini, there are only two independent transitions from a sand to a rock environment. How might the visual system need to evolve during such a transition? There may be differences in light levels, contrast, and color sensitivity. As expected, differences in light levels have been documented (Shumway, Hofmann, personal observations). The animal may need to make a trade-off between temporal resolution and spatial resolution, as both cannot happen simultaneously in the same neurons. A rock dweller may need enhanced object recognition and edge detection skills. Spatial memory may need to be enhanced, possibly at the loss of lateral line capabilities. Social tasks, too, may differ, given the increase in number of species and number of individuals in a more complex environment (Caley and St. John, 1996; Gray et al., 2000). To date, we have found differences in spatial resolution and spatial memory between sand- and rock-dwelling species and environments, as described below.

By selecting three ectodine species to control for the confounding variable of social organization, we found that habitat complexity was associated with differences in visual acuity (Dobberfuhr et al., 2005). Testing for optomotor/optokinetic responses and controlling for lens size, we compared three cichlid species differing in habitat preference (sand dweller: *X. flavipinnis*, intermediate habitats: *X. spiloptera*, rock dweller: *A. leptura*). All are monogamous/biparental species. At the 50% response point, the rock-dwelling species perceived a spatial frequency four times higher and a minimum separable angle (MSA) one-third that of species from less complex habitats. We speculate that rock dwelling favors adaptation for enhanced spatial resolution used in spatial navigation. Other researchers have demonstrated correlations between complex spatial tasks and brain structure size (e.g., bower building and brain size: Madden, 2001; bower building and cerebellar size:

Day et al., 2005; food storing in birds and rodents and hippocampal size: Lucas et al., 2004; Healy et al., 2005; home-range and hippocampal size: Healy et al., 2005).

2.8 Brain and brain structure size correlate with complex habitats

A number of studies on fishes have qualitatively associated ecological factors with brain structure. Differences in the size of sensory structures and integration centers such as the telencephalon and cerebellum were hypothesized to be linked with habitat type, feeding specializations, or locomotory activity (Kotrschal and Junger, 1988; Wagner, 2002; Eastman and Lannoo, 2003; Lisney and Collin, 2006; Yopak et al., 2007). However, these size differences were not systematically tested with the above variables. Only a few studies in mammals have quantitatively compared habitat complexity to the size of the brain or brain structures (chipmunks: Budeau and Verts, 1986; bats: Safi and Dechmann, 2005; Ratcliffe et al., 2006); these studies found that brain and brain structure size indeed correlated with complex habitats.

We compared relative brain and brain structure size, social organization, and habitat complexity among seven closely related ectodine cichlid species (Pollen et al., 2007). We eliminated the confounding factor of foraging behavior as much as possible by using only benthic feeders. The sand dwellers feed on insect larvae and other invertebrates in the sand; the rock dweller *A. leptura* feeds on algae on rock surfaces (Takamura, 1984; Konings, 1998). We used three different approaches to compare brain structures and habitat complexity: gross brain measures, fractions, and residuals. The results from fractions as well as independent contrasts (combining the results from both fractions and residuals) showed a significant positive correlation with the size of the telencephalon and both social and habitat measures. The size of the hypothalamus was negatively correlated with social measures, specifically social organization. Monogamous males had a smaller hypothalamus than polygynous males.

Brain size and cerebellar size were positively correlated with species number, which is correlated with habitat complexity; the medulla and olfactory bulb were negatively correlated with habitat measures. These results confirm, at a finer scale, the work by Huber et al. (1997) showing lake-specific differences among cichlid families in brain size and in the size of various brain structures relative to qualitative categories of the physical environment.

One surprising finding was that environmental and social factors differentially affect the brain (Pollen et al., 2007). Environmental factors correlated with more brain structures than did social factors. While five out of seven of the brain measures correlated with habitat measures, only two brain structures, the telencephalon and hypothalamus, correlated with social factors. Specifically, both social organization and number of individuals were positively correlated with telencephalic size; social organization was negatively correlated with hypothalamic size.

2.9 Spatial learning

We have just begun to examine whether innate cognitive differences correlate with the complexity of a species' environment. We compared the spatial abilities of the sand- and rock-dwelling species *Xenotilapia flavipinnis* and *Asprotilapia leptura*, respectively, in a sequential maze (Shumway et al., 2006). The maze contained both four local landmarks and two extramaze cues. The rock-dwelling fish completed the task more quickly and reached each landmark significantly faster than did the sand-dwelling species. While the rate of learning appeared the same, the rock-dwelling fish also had fewer wrong turns. These behavioral results correspond with preliminary studies showing that the hippocampal homologue, the dorso-lateral area of the telencephalon, or DI, is 20%–36% larger in two rock-dwelling species compared to two sand-dwelling species (Shumway et al., 2004; 2006). DI is known to be involved in spatial memory in fishes (Salas et al., 2003). Only a few studies in other systems have explored the relationship between physical complexity, cognitive ability, or brain differences across closely related species or populations. In fishes, Girvan and Braithwaite (1998) found behavioral differences in spatial learning ability and spatial strategies between pond and river populations of sticklebacks. In birds, food-storing species pay attention to spatial cues than to visual landmarks in a spatial memory task; non food-storers do not (Clayton and Krebs, 1994). Food-storing chickadees perform better in a spatial non-matching to sample task than non food-storing juncos do (Hampton and Shettleworth, 1996) and prefer spatial cues over color or pattern cues (Brodbeck, 1994). Neuroanatomical studies in mammals and birds have found a variation similar to that reported above (10% – 40%) in hippocampal volume correlating with differences in spatial ability among different species or between different sexes (Jacobs et al., 1990; Reboreda et al., 1996; Safi and Dechmann, 2005).

2.10 Plasticity's role

Do the observed cichlid species differences in complex brains and behavior simply arise over the course of evolution, or does experience contribute to the differences observed? To understand how adaptation occurs, we must tease apart the contribution of both environmental and genetic components of brain-behavior differences. Experience-dependent neuronal plasticity has been demonstrated in a variety of sensory areas and the hippocampus in both developing animals and adults (e.g., visual: Daw, 2004; somatosensory: Shumway et al., 1999, 2005). Experience-dependent plasticity has also been observed in behavioral tasks involving learning and memory (e.g., Clayton, 1994). In mammals, songbirds, and fish, social manipulations can affect neurogenesis, neuronal survival, and spine density in forebrain and midbrain areas (Coss and Globus, 1978; Fowler et al., 2002; Lipkind et al., 2002; Castellano et al., 2005). Fish may be more plastic than other vertebrate classes, given widespread neurogenesis which occurs throughout life in the telencephalon, cerebellum, and primary sensory areas (Zupanc et al., 2005; Adolf et al., 2006). Kihlslinger and Nevitt (2006) and Kihlslinger et al. (2006) found volumetric differences in the salmon telencephalon hatchery-reared in simple or complex environmental conditions. The proliferation rate of neurogenesis in salmon is also affected by environmental differences (Lema et al., 2005). Cichlids show considerable phenotypic plasticity. Plasticity has been demonstrated for visual and social behavior, neural structure and function, and feeding morphology (Liem and Osse, 1975; Meyer, 1989, 1993; Kröger et al., 2001; Insel and Fernald, 2004).

We explored the effect of social manipulations on visual behavior in pilot experiments by raising the sand-dweller *X. flavipinnis* in two social conditions: isolated or in a school (control). The animals for both conditions were raised on sand, their normal habitat. Each animal's visual acuity was tested at various developmental stages. Visual acuity has previously been shown to be experience-dependent in both fish (Wahl et al., 1993) and mammals (Prusky and Douglas, 2003). Social manipulations significantly influenced visual acuity as measured by minimal separable angle, but only within a critical early time period. Significant results were seen only at four months; by 12 months the difference between the two groups was negligible (Fig. 3A, B). We also explored the effect of environmental manipulations on visual behavior by raising the fry in both a simple (sand) and enriched (rock) environment

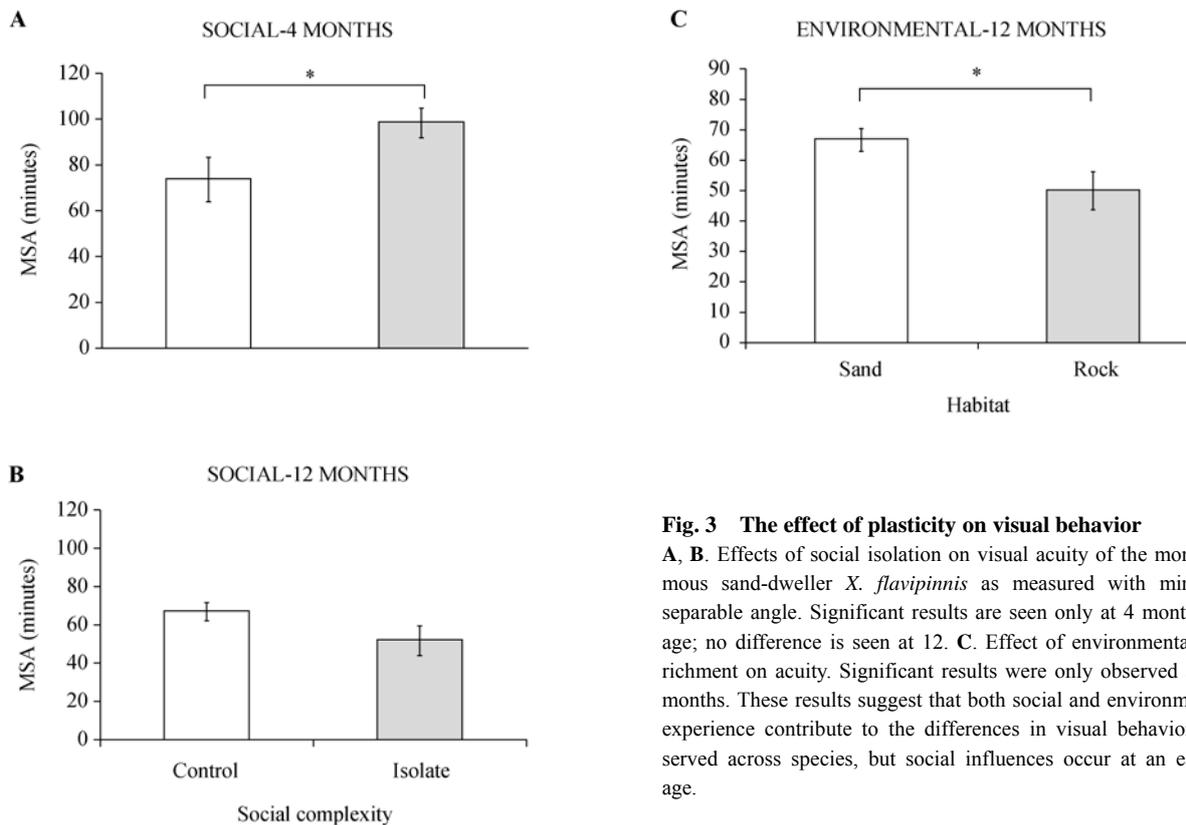


Fig. 3 The effect of plasticity on visual behavior

A, B. Effects of social isolation on visual acuity of the monogamous sand-dweller *X. flavipinnis* as measured with minimal separable angle. Significant results are seen only at 4 months of age; no difference is seen at 12. **C.** Effect of environmental enrichment on acuity. Significant results were only observed at 12 months. These results suggest that both social and environmental experience contribute to the differences in visual behavior observed across species, but social influences occur at an earlier age.

under normal social conditions (in a school) and testing visual acuity at various developmental stages. Pilot experiments showed a significant difference in visual acuity after 12 months, as measured by minimal separable angle (Fig. 3C). These results suggest that both social and environmental experience contribute to the differences in visual behavior observed across species, but that social influences occur at an earlier age.

3 Discussion

3.1 Comparing the two influences on brain and behavior

Do environmental or social forces exert a greater influence on cortical and brain expansion? The evidence remains inconclusive (Dunbar and Shultz, 2007). An animal does not exist in isolation. The genetic, neural, and behavioral evolution of an animal must be considered in context with how that animal both influences and is influenced by the environment and the social world around it. For example, an animal's social dominance can influence the social behavior of conspecifics (Insel and Fernald, 2004). Social dominance can even control the level of neurogenesis in the telencephalon in subordinate fish (Sørensen et al., 2007). Environmental conditions such as food scarcity or habitat structure can

also influence social organization, as shown for numerous mammalian species (Lott, 1991). The converse is also true. Species diversity and abundance can alter environmental conditions, particularly for those animals considered “ecosystem engineers” (Moore, 2006). In sum, multiple selective pressures drive the evolution of a larger brain and enhanced cognition.

Complicating matters is the fact that, at the individual level, environmental and social forces are not mutually exclusive. A number of papers have demonstrated correlations between cognitive flexibility and/or innovative feeding behavior and the size of the brain or brain structures (e.g., birds: Sol et al., 2005; rats: Ratcliffe et al., 2006; beetles: Farris, 2008). Reader and Laland (2002) showed that innovative tool use and social learning covaried in primates, and both behaviors correlated with increased brain size. Lefebvre and Sol (2008) argued that both social and physical variables may be driven by the same ecological factors, such as environments with unpredictable resources.

In cichlid fishes, we find that social variables, including species richness, species diversity, and abundance, are directly correlated with habitat complexity. While both forces shape the brain, social forces appear to influence visual behavior at an earlier stage than en-

vironmental ones. Taken together, the field data and the plasticity data suggest that some of the species-specific neural effects of environmental complexity could be the consequence of the corresponding social correlates.

However, environmental and social forces affect brains differently. Environmental forces exert a much broader effect on brain structures, suggesting allometric expansion of the brain structures in concert with brain size and/or coevolution of these structures. Co-evolution of the telencephalon and cerebellum occurs in primates (MacLeod et al., 2003), although the two structures appear to evolve at different rates (Finlay and Darlington, 1995; Finlay et al., 2001) and can vary in their extent of developmental plasticity (Zupanc, 2001; Shumway et al., 2005). In contrast, social forces, specifically abundance and social organization, are more selective, correlating only with telencephalic and hypothalamic expansion. Whether or not the difference in neuroanatomy would be reflected in function is unknown at this point, but cichlids could help us better understand the relationship between structure and function as well as the difference between these forces. Given the demonstrated impact of both habitat and social forces on brain structure, cichlids could also be used to explore whether the socially influenced areas of the brain are more or less plastic than those areas associated with habitat.

Although speculative, several lines of evidence suggest that social forces may cause qualitative changes in information processing during evolution, very different from environmental effects. In birds, no change is seen in telencephalic size as group sizes expand from solitary to colonial. However, telencephalic size significantly increases for birds that enact “transactions”, defined as between-individual social interactions or socially transferable cognitive tasks (Burish et al., 2004). In bower birds, brain size does not change with the complexity of the bower until the bower reaches a certain level of complexity (Madden, 2001). In humans, processing information about community members also shows qualitative differences. Anthropologists have shown that the size of human communities stays small if the community has only a single means of classifying members. As soon as the community identifies a second axis for classification, the community can become dramatically enlarged (Carneiro, 2000).

3.2 Future directions

To date, all of our research has been correlative. Correlations, of course, do not equal causation. Future efforts include, first, identifying the most significant ecological cues underlying the effect of habitat com-

plexity in cichlid fishes. To date, we have little understanding of what visual features really matter to animals in their natural environment, or how species-specific this may be (i.e., their “umwelt” or subjective world; Uexküll, 1985). Second, we want to further explore the developmental influence of social and environmental forces to determine how much plasticity contributes to the species-specific differences found. Behavioral drive is thought to be an important evolutionary force underlying cichlid evolution (Seehausen, 2000). Could the capacity for plasticity distinguish those clades or families that are most speciose? Third, plasticity experiments could also help resolve the question of whether it is the importance of the complexity of the visual scene or the complexity of the spatial task that matters. In other words, if the visual environment differs but the behavioral requirements do not, would brain changes be seen? Fish could be raised in a two-dimensional complex visual scene (rock) versus a two-dimensional sand scene, but with no complexity in space. Fourth, my collaborator Hans Hofmann will use genomics to tease apart which social cues lead to telencephalic expansion in monogamous species: parental care or pair bonding. Finally, the use of modelling based on information theoretic principles (Bialek, 1987; Laughlin et al., 1998) will enable us to predict and deepen our understanding of how complex brains and behaviors evolve. Specifically, modeling coupled with behavioral experiments should help us better understand the differences in information processing for social and environmental tasks.

3.3 Conclusions

In this review, I have shown that both behavioral and brain changes correlate with social organization and habitat complexity in African cichlid fishes. The influence of these forces is both innate and experientially induced. To advance our understanding of the mechanism by which social or environmental forces affect brain and behavior will require the use of closely related species, quantification of complexity, hypothesis testing restricting analysis to a single variable (e.g., foraging behavior, habitat complexity, spatial task complexity, social complexity) and path analyses to explore the order of importance of such variables. Plasticity experiments may also help resolve the order of timing and influence of socio-ecological variables on the brain. Finally, we will need new experimental paradigms exploring the cognitive and survival value of brain and brain structure changes both in the laboratory and in the wild (e.g., Lingo and Szedlmayer, 2006; Sol et al., 2007).

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