Fish Plasticity

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JAWS AND FEEDING MECHANICS

Think "adaptive radiation," and island-dwelling species, such as Galápagos finches and Hawaiian fruit flies, probably spring to mind. Another impressive example of this type of rapid speciation is the cichlid: 1400 species of this fish are found in the rift lakes of Africa. The malleability of form and function in these animals makes cichlids ideal subjects for studying evolutionary questions—for example, What are the underlying mechanisms that make such malleability possible?

Craig Albertson, of the Forsyth Institute and Harvard School of Dental Medicine, and colleagues examined the biomechanics of jaw development and its genetic basis in two species of cichlid fish with different feeding strategies (see the 8 November issue of *Proceedings of the National Academy of Sciences*). The species with better biting jaws (*Labeotropheus fuelleborni*) feeds on algae attached to hard substrates. The suction-feeding species (*Metriaclima zebra*) has a long lower jaw that is adapted for devouring mobile prey.

Cichlid jaws, like those of all bony fish, operate by opposing lever systems, one out-lever and two in-levers for opening and closing the jaws. When the ratio of the in-lever to the out-lever is high (as in *L. fuelleborni*), the jaw has greater mechanical advantage and therefore generates more force for biting. When that ratio is low, as it is in the long jaws of suction feeders (such as *M. zebra*), the mechanical advantage is small, which translates into an ability to generate greater velocity.

When the scientists mapped the mechanical advantage of closing and opening, they found two and four loci, respectively, on four different chromosomes. The loci controlling the levers themselves (two for the out-lever, three for the closing in-lever, and five for the opening in-lever) mapped to the same four chromosomes plus two others, with varying degrees of overlap between out-lever loci and those for either of the in-levers. There was no overlap between loci for the opening and closing in-levers, however.

To form a functioning jaw, the genes that determine the shape and mechanics of cichlid jaws must be integrated during development. Their dispersal throughout the genome suggests they are genetically modular traits of jaws that are integrated to different degrees, such that, for example, as the closing in-lever gets longer, the out-lever shortens, and vice versa. The out-lever and opening in-lever are less tightly integrated, and the opening and closing in-levers are decoupled completely, allowing them to be inherited independently.

Such genetic plasticity has made the versatile feeding adaptations seen in this speciose group of fish possible. Just how moldable are cichlid jaws? One of the loci linked to the jaw-closing system, the gene for a bone morphogenetic protein (*bmp4*), plays a major role in craniofacial development in vertebrates. Expression of this gene was followed during jaw development in both species, and levels of expression were experimentally manipulated in another species (*Danio rerio*), to determine the role of this protein in jaw morphogenesis. The outcome: When more *bmp4* is expressed, jaws form with longer coronoid processes—that is, longer closing in-levers—and greater mechanical advantage.

MATING AND SOCIAL DOMINANCE

Another line of inquiry into the evolution of cichlids has to do with their reproductive behavior. Scientists studying a species (*Astatotilapia burtoni*) in which social dominance regulates male fertility have looked at the relationship between social cues and reproduction. Sabrina Burmeister and Russell Fernald, of Stanford University, and Erich Jarvis, of Duke University Medical Center, have examined the behavioral and physiological responses of subordinate males presented with an opportunity to become socially dominant (see the November issue of *PLoS Biology*).

The physical characteristics of male dominance are reversible in this species. In the lab, stably dominant males lose their brilliant coloration overnight, regaining it when the lights go on each morning. If an hour before "dawn" a dominant male is removed from an experimental tank with four females and one subordinate male, the subordinate male ascends in rank within minutes of realizing his opportunity. He adopts the bright coloration and aggressive behaviors characteristic of a dominant male, and he begins courting females.

Burmeister and colleagues compared the physiological states of subordinate and dominant males by measuring the expression of a transcription factor (*egr-1*), which they believe is the first step in a cascade leading to the production of sex hormones and changes in physiology. Ascending males showed a twofold increase in *egr-1* expression over levels expressed by stable subordinates or stable dominants, even though the latter showed all other signs of dominance. Expression of *egr-1* in ascending males was also localized in a specific part of the preoptic region of the hypothalamus, where the neurons that regulate gonadotropin-releasing hormone (*GnRH1*) gene expression are active.

Subordinate males that were not given the same social opportunity showed none of the changes seen in ascending males. The cichlids' behavioral and physiological responses to reproductive social cues, previously thought to take days, were switched on in a matter of minutes.

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