

# Specialized morphology for a non-specialized diet: Liem's paradox in an African cichlid fish

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## Abstract

Cichlid fishes of the East African Great Lakes represent some of the most diverse vertebrate faunas in the world, and trophic specialization, the specific adaptation of feeding structures to one type of prey, is often used to explain the coexistence of these closely related species. However, Liem's Paradox suggests that organisms with specialized phenotypes may act primarily as generalist feeders in nature, which can create a mismatch between diet and morphology. Our goal was to study the diet of a widespread African cichlid, *Astatoreochromis alluaudi*, over the course of 1 year to test the hypothesis that the molluscivore-like morphology of this species is not an appropriate indicator of diet choice. Lake Saka, in Uganda, was sampled monthly throughout 2006, and stomach content analyses were performed on preserved specimens using established techniques to identify the relative importance of various prey items in the diet of *A. alluaudi*. Stomach content analyses indicated an omnivorous diet in all months, consisting mostly of insects, fish, and plant matter, whereas snails accounted for only a small portion of their overall diet. Although trophic morphology in this species is a plastic trait, specimens from Lake Saka exhibit a molluscivore-like morphology. Our data suggests that the morphology of this generalist feeder may have developed to exploit non-favoured resources, a clear example of Liem's Paradox. This study emphasizes the importance of examining both stomach contents and trophic morphology before inferring the feeding ecology of a species.

## Keywords

*Trophic specialization, African cichlids, Molluscivore, Omnivore, Morphology.*

## Introduction

Of all the freshwater fish species in the world, the cichlid fishes of East Africa are arguably the most diverse, well-known, and well-studied group (McKaye and Marsh 1983). Over 600 species, half of which are endemic to the area, were found in one watershed in the Lake Victoria basin alone (Alphen et al. 2003). It has long been hypothesized that specialization in feeding (trophic) morphology and diets of these fishes is an important factor contributing to their radiation within these watersheds (Liem 1991). Furthermore, trophic specialization has been used to explain the coexistence of such a large number of closely related organisms and the existence of the multitude of endemic species present in any given lake (Fryer and Iles 1972, Barlow 2000). For example, cichlids from the African Great Lakes are known to include piscivores (Mbabazi et al. 2004), paedophages (fish egg and embryo-eaters), insectivores (Hoogerhoud 1987), crustacean-eaters, molluscivores (Greenwood 1964), lepidophores (scale-eaters, Hori 1993), herbivores, epilithic and ephiphytic algae-eaters, phytoplanktivores (Katunzi et al. 2003), zooplanktivores (Goldschmidt et al. 1993), and detritivores (Greenwood 1959). *Astatoreochromis alluaudi* is a widespread East-African cichlid (Hoogerhoud 1984, Huysseune 1995) that has two distinct and well described pharyngeal jaw morphologies, which vary depending on diet. Cichlid fishes possess a second pair of jaws, which aid in prey processing, located deep in their buccal cavity known as pharyngeal, or throat jaws. Large-jawed, hypertrophied morphs of *A. alluaudi* have been associated with a snail-eating, molluscivorous diet, whereas small-jawed, non-hypertrophied morphs are believed to feed on softer food items such as insects and plant material (Smits et al. 1996). Studies have shown that this morphological differentiation is a plastic trait dependent on juvenile prey choice, irrespective of paternal phenotype (Greenwood 1964, Hoogerhoud 1986).

Although it is a widespread cichlid in East Africa, *A. alluaudi* has been most extensively studied in Lake Victoria, where it consumes primarily snails (Witte 1981), and as a

result, it is largely assumed that this species is a molluscivore (Greenwood 1964). However, *A. alluaudi* has also been reported to feed on various prey resources, and is known to prefer insect prey if it has access to this resource (Slootweg et al. 1994). Since jaw morphology in *A. alluaudi* is a developmental trait that apparently canalizes early in an individual's lifetime, a fish exposed to hard-bodied food items during its early life stages will develop molariform morphology even if it routinely feeds on softer prey items (Smits, 1996). Similarly, in times of resource scarcity, even highly specialized fishes have been observed to switch to an omnivorous diet in order to meet their energy requirements (McKaye and Marsh 1983). Thus, it is possible that seasonal fluctuations in resource abundances at a site may influence jaw morphology and diet in *A. alluaudi*, particularly if there are certain periods of time during which the cichlid must consume snails in order to survive even if it feeds on other prey types preferentially the majority of the year.

In Lake Saka, a crater lake located in western Uganda, morphological analyses performed on *A. alluaudi* specimens (L.J. Chapman unpubl. data) revealed that this particular population has relatively well developed hypertrophied jaws not characteristic of *A. alluaudi* that are fully insectivorous (Figure 1). However, many cichlid fishes with specialized feeding structures have been reported as generalist feeders in field studies, questioning the accuracy of studies focusing solely on morphology as a predictive tool.

The general goal of our study was to describe variation in the diet of *A. alluaudi* from Lake Saka, Uganda to explore whether morphology is a good indicator of feeding habits in this species. To meet this goal, we analyzed stomach contents of fish collected monthly in 2006 from Lake Saka, Uganda. We believe that this study has important implications for ecological studies of fish, which often categorize species based on their trophic structures without rigorously examining their feeding ecology.

## Materials and Methods

Lake Saka (0 40'N, 30 15'E, Figure 2) is a crater lake located near Fort Portal, Uganda. This region of East Africa is characterized by two wet and two dry seasons per year. In Lake Saka, surface dissolved oxygen varies from 6 mg l<sup>-1</sup>

to supersaturation (greater than 12 mg l<sup>-1</sup>) throughout the year, often exceeding 15 mg l<sup>-1</sup> in the surface waters. This is thought to reflect enhanced phytoplankton productivity over the past 3 decades (Crisman et al. 2001). Water column anoxia does not seem to occur in the northern section of the lake where *A. alluaudi* were collected (approximately 2 m depth) but have been reported in the deeper areas of the lake, particularly in the southern section where there is a very small but deep crater (>12 m) (Crisman et al. 2001). Specimens were collected bimonthly from the northern part of Lake Saka, using baited metal minnow traps set between 10:00 am and 2:00 pm from January to December 2006. Due to issues concerning site access, no samples were collected during March. Fish were euthanized with MS222, preserved in 10% formalin, and transported back to McGill University for stomach content analysis.

Fishes of varying standard lengths, as measured from the tip of the snout to the start of the caudal fin rays, were chosen to obtain a representative sample of the population; and the two samples were combined within each month to provide a larger and more representative monthly sample. In total, 138 fishes with non-empty stomachs were examined. For most months, all fishes were sampled; however, for months with large numbers of collected fish, we subsampled 10 fish with non-empty stomachs. Sample sizes for each month ranged from a minimum of 5 stomachs (February) to 19 stomachs (November), but on average, 12 non-empty stomachs were analyzed per month. Fish stomachs were dissected out, and stomach fullness was visually assessed using the following criteria: level 1, empty stomach; level 2, 1-25% full; level 3, 26-50% full; level 4, 51-75% full; level 5, 76-100% full. Stomach contents were observed under a dissecting microscope (LEICA MS5), and food items were separated and identified taxonomically to order level resolution when possible (McCafferty 1981). Food items were sorted into one of the following categories: fish (mature/juvenile individuals and fish larvae), gastropods, insects (primarily Ephemeroptera and Diptera), plant matter (mostly algae and macrophytes), oligochaetes, and zooplankton.

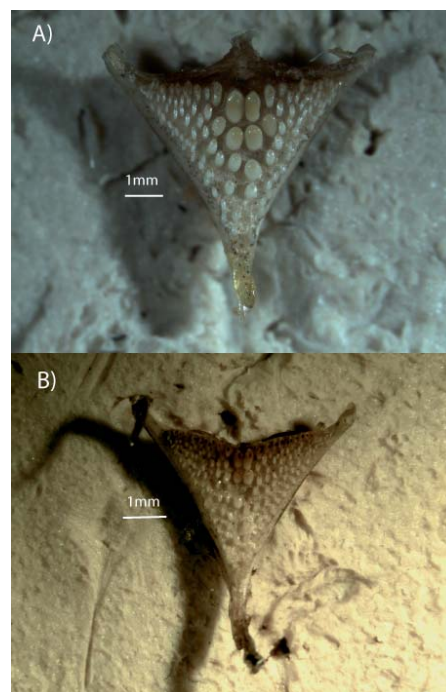
We quantified each item by using a modified version of the points method (Hynes 1950). First, the percentage volume of each food item was visually assessed by estimating how much it contributed to the total amount of food found in a given stomach. Each food item found in an individual fish was allotted a number of points based on its relative percentage rounded to the nearest 10 percent. To take into account the percent fullness of each stomach, these points were then multiplied following fullness criteria: level 2, by 0.25, level 3; by 0.5, level 4; by 0.75 and level 5; by 1. Finally for each sample, the total number of points per category was calculated and divided by the total number of non-empty stomachs in the sample.

We used linear regression on the points results to evaluate whether the mean monthly points for fish, insects, plant matter, or gastropods correlated with seasonal rainfall. This was done in two ways: we used the monthly rainfall and the 2-month running average, which takes the accumulated rainfall from the previous month into consideration.

## Results

Over the course of the year, *A. alluaudi* consumed a variety of prey items in varying amounts (Figure 3). Overall, fish formed the most abundant category, and comprised nearly half of the annual diet of *A. alluaudi*. The fish remains found in the sto-

machs appeared to be cichlids, but no further analyses have been done to identify the species of cichlid. The plant matter food category consisted principally of algae and macrophytes. Debris consisted primarily of small rocks or sandy particles; which were probably taken unintentionally while feeding on insects or plants (Hyslop 1980). Both plants and insects appeared to be important resources in the diet of *A. alluaudi* and were often the second or third dominant food types encountered each month (Figure 4).



**Figure 1:** Dorsal view comparison of the lower pharyngeal jaw of *A. alluaudi* specimens from (A) Lake Saka and (B) Lake Nabugabo. Both fish specimens have standard lengths of  $63.95 \pm 2.00$ mm. Lake Nabugabo is a well-studied site where snails are absent, and *A. alluaudi* routinely feeds on insects and fish.

Although gastropods were present in the stomachs consistently throughout the year, they did not seem to form a major component of the diet of *A. alluaudi*, and in most months, they ranked as the third or fourth most abundant prey (Figure 4). Overall, gastropods contributed less than 5% of the annual diet of *A. alluaudi* (Figure 3). Oligochaetes and zooplankton only contributed to 10% of the overall diet (Figure 3). Some stomachs were found to have exclusively zooplankton or worms, which eliminates the possibility that *A. alluaudi* unintentionally fed on these resources. Linear regression analyses indicated no significant relationship between four of the important food categories and rainfall: fish ( $F=0.340$ ,  $p=0.574$ ), insects ( $F=1.025$ ,  $p=0.338$ ), plant matter ( $F=0.063$ ,  $p=0.807$ ), and gastropods ( $F=1.257$ ,  $p=0.291$ ). However, our analysis of running rainfall average indicated a weak correlation with percentage piscivory per month ( $R^2=0.301$ ,  $p=0.08$ ).

## Discussion

### Feeding specialization and Liem's paradox

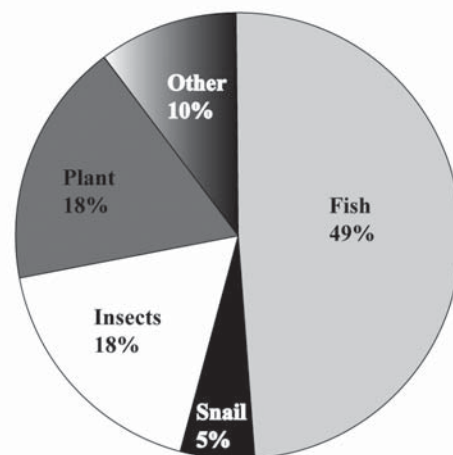
Our results provide evidence suggesting that *A. alluaudi* from Lake Saka are generalist feeders, consuming mostly other small cichlids, insects, and plant matter. Over the year of study, we found that only a very small portion of their diet was comprised of snails. This finding was unexpected based on our morphological studies which demonstrate that this population has prominent pharyngeal jaws usually associated with

a more, although not exclusively molluskivorous diet.

The lack of a tight correspondence between diet and morphology found in our study has been observed in other cichlid species (Katunzi 1983) as well as in Darwin's finches (Tebbich et al. 2004), and is often referred to as Liem's paradox (Liem 1980). In essence, Liem's theory suggests that specialized phenotypes are retained to exploit less-favored food sources rather than favored resources. This adaptation is possible if the specialized phenotype is still efficient in processing other resources allowing individuals to feed on various foods, especially when the favored prey resources are limited. In the case of *A. alluaudi*, large jaws may be used to feed on snails when fishes or insects are rare.

The likelihood of specialized feeders being able to efficiently switch between resources was believed to be small, especially when the resources required different feeding techniques to be eaten (Barel 1983). However, studies of Darwin's finches have reported these apparently specialized birds switching both prey base and feeding technique in response to fluctuating resource abundances (Schluter 1982, Tebbich et al. 2004). In the case of aquatic species, it was long hypothesized that biting and sucking feeding techniques were only compatible to a certain extent because of anatomical demands (Barel 1983). However, recent studies refute this presumed trade-off (Van Wassenbergh et al. 2007), and have shown that some fish that seem morphologically adapted to be biters are as effective in sucking prey as are sucking specialists (Bouton et al. 1998, Van Wassenbergh et al. 2007). The sucking technique is an effective way of consuming most insect larvae such as Diptera larvae, which is a major food source of *A. alluaudi*. Since insects comprise 18% of *A. alluaudi*'s overall diet, we assume that morphological specialization in *A. alluaudi* does not constrain its ability to feed on insect larvae, a potentially favoured resource. Flexible omnivory might allow *A. alluaudi* to better coexist with other species by reducing niche overlap and direct interspecific competition. Omnivory may also be adaptive from an optimal foraging perspective. According to optimal foraging theory the caloric value obtained from a potential prey item must exceed the time and energy costs of catching and processing a given prey (Robinson and Wilson 1998). In other words, calorie-rich food may not be consumed by certain species if there are lesser-quality but easily-handled

foods available. It is reasonable to believe that the energy pay-off as well as the handling time differs for all the prey items consumed by *A. alluaudi*, and that these foraging considerations influence a fishes diet, especially in a spatially and tem-



**Figure 3:** Average diet composition of *A. alluaudi* in Lake Saka over all months.

porally variable habitat. However, specific details concerning the energetic quality of possible prey in this system have not been documented and were beyond the scope of this study.

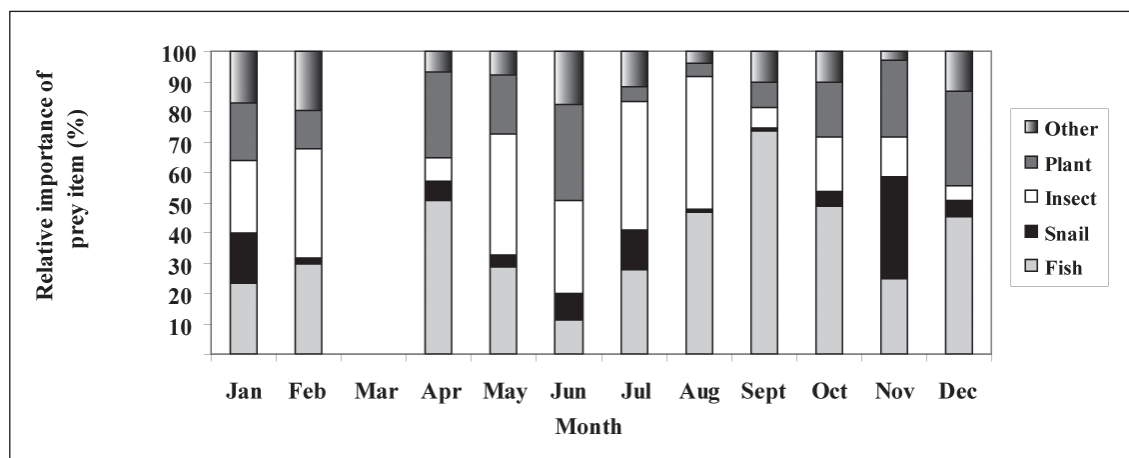
In proposing that *A. alluaudi* in Lake Saka are very omnivorous and that mollusks comprise a small component of their diet, we assume that our analysis of diet was relatively unbiased. The analysis of stomach contents as a means to describe seasonal variation in an organism's diet or dietary comparison between species is a standard and widely used practice in fish ecology (Hynes 1950). However the appropriate method often depends on the organism of study, the mechanical digestion apparatus, and the types of prey consumed. We selected the points method for characterizing the diet of *A. alluaudi* since the food experiences a high degree of mechanical processing in the pharyngeal jaws before entering the stomach. It takes into account the stomach fullness, but has been criticized for its subjectivity (Hyslop 1980). Regardless of the method used, overrepresentation or underrepresentation of some items may be induced by different digestion rates. For example, crustaceans and fish remains, principally scales take longer to be digested and thus tend to be overrepresented in analyses (Van Wassenbergh et al. 2007). The abundance of scales found in *A. alluaudi* stomachs could be a reflection of this bias; however, we believe that these potential limitations would not have altered the main results of this study.

#### *Hypertrophied morphology, architectonic interdependency and dissolved oxygen*

Another plausible explanation for the retention of molluskivorous morphology in *A. alluaudi* resides in the concept of architectonic interdependency. The cranial musculo-skeletal system of fishes is extremely complex and necessary for various vital functions such as capturing and processing prey, gill ventilation, protection to vital organs, and locomotion. Thus, many of these functions are interdependent through architectonic relations, and an adaptive response to one structure might consequently affect another. The large volume occupied by the specialized pharyngeal jaws of *A. alluaudi* in Lake Saka has multiple direct and indirect effects on other head structures, such as gill size. Dissolved oxygen (DO) levels in the shallower waters of the hyper-eutrophied Lake Saka are high, and



**Figure 2:** Map of Uganda showing the location of Lake Saka.



**Figure 4:** Percent importance as determined by the points method of major food categories in the stomachs of *A. alluaudi* in 2006.

the lake almost never experiences anoxic conditions in the surface waters (Crisman et al. 2001). The specimens collected in this study were from shallow waters, where oxygen content in the upper waters tends to be supersaturated during the day. Many haplochromine species known to have mollusk-associated pharyngeal jaws are, in fact, limited to water less than 12 m deep (Greenwood, 1960; Witte, 1981). One plausible explanation for this lies in their morphocranial architecture: very large pharyngeal jaws constrain larger gill sizes that develop in low DO. The relationship between gill size in fishes and dissolved oxygen levels has been well studied for several species of African fish (Chapman et al. 1995, Schaack and Chapman 2003, Chapman et al. 2006). Since *A. alluaudi* populations from Lake Saka are not constrained by low DO concentrations and are characterized by a relatively small total gill surface area (Chapman et al. 2007) there is no evidence for a spatial trade-off which would constrain jaw development.

#### Seasonal variation in resource availability

The feeding behavior of *A. alluaudi* did not show any clear patterns correlated directly with rainfall variation. However, fish prey appeared to be more abundant in the diet of *A. alluaudi* during rainy months, particularly small larval and juvenile fish. Reardon and Chapman (2008) have found that spawning peaks in the cichlid species from this region are associated with seasonal peaks in precipitation. Hence, during wet seasons, juvenile fish density may be particularly high, offering an easy and rich food source for piscivorous species. More detailed studies of the relationship between seasonal dietary change and prey availability will be required to fully explore this idea.

#### Conclusion

Although cichlids are among the best-studied families of freshwater fishes in the world, there is still much that is unknown about the ecology of these organisms. East African cichlids from the Great Lakes are often used as a model system to study evolutionary questions concerning speciation (Fryer 2001, Alphen et al. 2003), coexistence (Fryer and Iles 1972, Ribbink 1991, Genner et al. 1999b), and the origin of ecological specialization (Bouton et al. 1997, Genner et al. 1999a, Mbabazi et al. 2004). However, many species endemic to the Lake Victoria watershed have yet to be described, and the role of trophic specialization in promoting the coexistence of closely-related species has been increasingly called into question (Genner et al. 1999b, Katunzi et al. 2003). This study provides evidence to suggest that *A. alluaudi* from Lake Saka is a generalist feeder whose diet is principally composed of insects, fish, and plant

matter. This result is unexpected based on earlier studies of *A. alluaudi* jaw morphology from Lake Saka, which are not characteristic of insect-eaters. Based on this morphology, we anticipated snails to be an important food source for this population. However, *Astaroerochromis alluaudi* seems to be another case of Liem's paradox, where when favoured prey are rare fishes develop a specialized morphology to exploit a non-favoured resource. These results highlight the importance of combining dietary analyses with morphological studies in order to fully understand the feeding ecology of a species.

#### Acknowledgements

The authors would like to thank Laurence Piche for laboratory assistance, as well as Professors G. Fussmann and D.J. Lewis for their help on zooplankton and insect identification. We would also like to thank the government of Uganda for granting permission to carry out this research. Photos and Maps are courtesy of V. Tzaneva and F. Crispo. Funding for this research was provided by NSERC discovery grant and Canada Research Chair funds to L. J. Chapman.

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