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## Hypoxia tolerance of two haplochromine cichlids: swamp leakage and potential for interlacustrine dispersal

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### Synopsis

The ability to tolerate hypoxia in some haplochromine cichlid fishes contributes to the richness of habitats occupied by the lineage and may be important in interlacustrine dispersal through swampy channels. Lacustrine members of the genus *Astatotilapia* tend to be ecologically plastic but are rarely encountered in the interior of dense swamps. A notable exception is seen in the swamp corridor that joins Lake Kabaleka with Lake George, Uganda, where one species (*Astatotilapia* ‘wrought-iron’) is abundant, and a second species, *A. aeneocolor*, is rare. Both species are abundant in the open waters of the main lake. In this paper, we compare physiological (oxygen consumption) and behavioral indicators of hypoxia tolerance between *A.* ‘wrought-iron’ from swamp and open-water habitats and between the two species of *Astatotilapia*. When exposed to progressive hypoxia, all fish used aquatic surface respiration (ASR); however, swamp-dwelling *A.* ‘wrought-iron’ showed lower gill ventilation rates prior to the initiation of ASR, higher pre-ASR aggression rates, higher swimming speed during ASR, and a higher rate of bubble exchange than both the open-water group of *A.* ‘wrought-iron’ and *A. aeneocolor*. These differences may reflect interpopulational variation in selection pressure for low-oxygen tolerance between swamp and open-water habitats. Several lines of evidence suggest that *A.* ‘wrought-iron’ was in general more hypoxia tolerant than *A. aeneocolor*. These include a lower ASR<sub>90</sub> threshold, a drop in gill ventilation rate with the onset of ASR, and lower rate of equilibrium loss under extreme hypoxia in *A.* ‘wrought-iron’. The routine metabolic rate and critical oxygen tension did not differ between swamp-dwelling and open-water *A.* ‘wrought-iron’, or between *A.* ‘wrought-iron’ and *A. aeneocolor*. Comparative data on the ASR thresholds and critical oxygen tensions of the *Astatotilapia* species from Lake Kabaleka and other East African cichlids suggest intermediate hypoxia tolerance. Nevertheless, our study suggests that some generalized lacustrine haplochromines may ‘leak’ through swamp corridors even under relatively extreme conditions.

### Introduction

Haplochromine cichlids are widespread, ecologically diverse, and often abundant in East African freshwaters (Fryer & Iles 1972, Greenwood 1980). Most species are lake-dwellers, and owing to numerous intralacustrine speciation events, this group has become the poster taxon for adaptive radiation in vertebrates (Dominey 1984, Fryer 1996, Kaufman et al. 1997). The Lake

Victoria radiation of endemic haplochromine cichlids has produced an estimated 600+ species and represents part of a larger Lake Victoria region superfamily, a monophyletic community spread across the watersheds of the region (Fryer & Iles 1972, Greenwood 1981, Meyer 1993, Kaufman 1997). Biogeographical links occur between lakes Victoria and Kyoga, lakes Edward and George, and between lakes Edward–George and Kivu; however, endemic species occur in each lake.

Haplochromine cichlids occupy a wide diversity of habitats within lakes. For example, prior to the increase in the introduced predatory Nile perch, *Lates niloticus*, population in Lake Victoria, haplochromine cichlids were found in open waters, structurally complex rocky habitats, littoral vegetated areas, and dense swamps (Welcomme 1970, Witte et al. 1992a,b). Faunas of lower species richness are also found in fast-flowing riverine waterways (Lowe-McConnell 1991) and in slow-moving swampy channels that link lacustrine habitats (Chapman et al. 1996b).

There are many features of haplochromine cichlids that may have contributed to their richness and widespread distribution within the Lake Victoria region. One character that is just beginning to receive attention is the interspecific variation in tolerance to low dissolved oxygen concentration. Hypoxia is widespread in lakes and rivers of the Lake Victoria region, particularly in the dense papyrus, *Cyperus papyrus*, and *Miscanthidium violaceum* swamps, where the canopy limits light and mixing of the water, and contributes large amounts of decomposing organic material (Carter 1955, Beadle 1981, Chapman et al. 1998, 2000). The ability to tolerate hypoxia in some haplochromine cichlids has clearly contributed to the diversity of habitats they occupy. Hypoxia-tolerant species may find refuge from predators (Chapman et al. 1995, 1996a,b, Rosenberger & Chapman 1999), gain access to food resources not normally found in open-water habitats, or use wetlands as dispersal routes into new habitats.

Examining the patterns of hypoxia tolerance among species and lineages may also be important to our understanding of faunal mixing among lakes. Lakes in the basin are often connected by swamp corridors, and passage by cichlids through these corridors is constrained by hypoxic stress, among other things (Chapman & Liem 1995, Chapman et al. 1995, Kaufman et al. 1997). However, such dispersal events appear to be critical in shaping the biogeography and evolution of the fauna. Ecologically plastic and evolutionarily 'explosive' groups may seed new radiations when they invade new lakes where they can quickly track new habitats and food resources through epigenetic plasticity (Kaufman 1997, Kaufman et al. 1997). *Paralabidochromis* spp. is one example of an explosive taxon that exhibits both species richness and morphological differentiation (Kaufman 1997). Kaufman (1997) also suggested that many of the truly lacustrine fishes still currently placed in *Astatotilapia*<sup>1</sup> may fall in

<sup>1</sup> The genus *Astatotilapia* includes a fluvial group that forms a monophyletic lineage (Lippitsch 1993). A lacustrine group of

this category, although the genus is not a monophyletic entity (Lippitsch 1993) and is in need of taxonomic revision. These two genera (*Paralabidochromis* and lacustrine *Astatotilapia*) are very rarely encountered in the interior of dense swamp corridors. One notable exception is seen in the swamp corridor that joins Lake Kabaleka with Lake George, Uganda, where we found two species of generalized lacustrine *Astatotilapia* up to 1500 m into the swamp corridor from the Lake Kabaleka side. Within the swamp corridor, one species was very abundant, and the other was very rare. The hypoxia tolerance of these two species may explain their occurrence and differential abundance in the dense swamp interior.

In this paper we evaluate the potential of hypoxia tolerance as a predictor of persistence in hypoxic swamp corridors. First, we compare physiological (oxygen consumption) and behavioral indicators of hypoxia tolerance between the two species of *Astatotilapia* from Lake Kabaleka. We predicted that the species or populations abundant in the swamp corridor would exhibit greater hypoxia tolerance than the species or populations found primarily in the open waters of the main lake. Second, we compare our data on the two *Astatotilapia* species from Lake Kabaleka to available data on a suite of East African cichlid species to evaluate their relative hypoxia tolerance.

## Methods

### *Study site and species*

Lake Kabaleka (0° 16' N and 30° 15' E, approx. 100 ha, 1050 m above sea level) is a shallow lake that rarely exceeds 2–3 m in depth and grades into a dense papyrus wetland at the south end of the lake, which extends for 20 km south to Lake George (Figure 1). In the first 2 km, water discharges through an open channel that flows through the dense papyrus, before it is closed in by vegetation. Dissolved oxygen (DO) levels are low in the papyrus swamp channel, and there is a marked stratification in both the open water and the swamp channel (Table 1). Submerged macrophytes are absent. Conductivity, temperature, and pH are all slightly higher in the open water than in the dense swamp interior.

*Astatotilapia* can be distinguished from the riverine group based on scale and squamation characters (Lippitsch 1993). Lippitsch states that it seems probable that most of the lacustrine members are closely related and suggest that a new genus be established for this group.

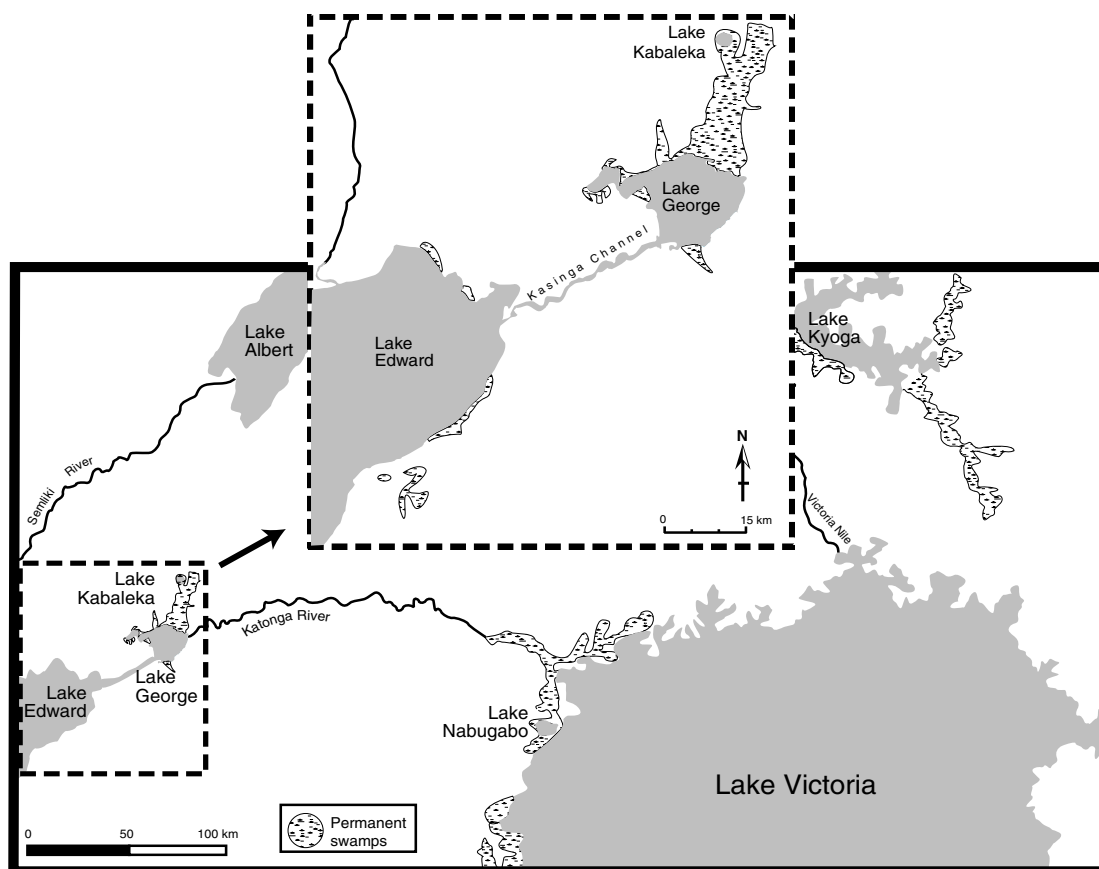


Figure 1. Map of the Lake Victoria region of East Africa showing the location of Lake Kabaleka and the swamp corridor that separates lakes Kabaleka and George.

Table 1. Mean dissolved oxygen level, water temperature, pH, and conductivity of several open-water and swamp sites within Lake Kabaleka, Uganda ( $\pm$ S.E.). Data were collected on 1 day in August 1997 and 1 day in May 1998. Papyrus swamp measurements were taken beyond 1 km into the swamp channel, while 'open-water' measurements were taken in the open lake.

Water depth (m)	Dissolved oxygen ( $\text{mg l}^{-1}$ )	Water temp. ( $^{\circ}\text{C}$ )	pH	Conductivity ( $\mu\text{S cm}^{-1}$ )
<i>Papyrus swamp</i>				
0	$1.57 \pm 0.95$	$23.5 \pm 0.27$	$7.36 \pm 0.19$	$241.1 \pm 1.1$
1	$0.53 \pm 0.22$	$23.1 \pm 0.12$		
<i>Open water</i>				
0	$7.94 \pm 1.44$	$28.7 \pm 1.25$	$7.93 \pm 0.36$	$315.7 \pm 22.1$
1	$5.51 \pm 1.07$	$25.3 \pm 0.66$		
2	$2.77 \pm 2.11$	$23.7 \pm 0.10$		

We focused on the two most abundant haplochromine cichlid species in Lake Kabaleka: *Astatotilapia aeneocolor* and *A. 'wrought-iron'*. *A. aeneocolor* is a species described from Lake George (Greenwood 1973). *A. 'wrought-iron'* is an undescribed haplochromine cichlid that is likely endemic to the lake

(Kaufman et al. unpublished data), though the introduction of tilapiines throughout Uganda precludes a definitive origin because of the possibility of accidental transfer. Both haplochromine species are very abundant in the lake's open waters (catch ratio of *A. 'wrought-iron'* to *A. aeneocolor* = 0.97:1),

but *A. aeneocolor* is much less abundant than *A. 'wrought-iron'* in the dense interior of the fringing swamp (catch ratio = 10:1). We have found three other haplochromine cichlids in the lake: an undescribed species, and two widespread swamp-dwelling species, *Pseudocrenilabrus multicolor victoriae* and *Astatoreochromis alluaudi*.

#### *Fish collections and holding conditions*

We captured male cichlids in Lake Kabaleka from May to July of 1998 with minnow traps and gill nets. We did not use female cichlids because it was not possible to identify them to species in the field. We collected *A. 'wrought-iron'* from both the open waters of the main lake and the dense interior of the fringing swamp, approximately 1500 m beyond the mouth of the channel. *Astatotilapia aeneocolor* was only collected from the main lake, because it was so rare in the dense swamp interior ( $n = 2$  specimens). Fish were transferred to the Makerere University Biological Field Station and held under shade cover in plastic tanks to minimize temperature fluctuations. Fish were maintained in river water to prevent high oxygen consumption rates by phytoplankton at night. The water was collected from the Dura River, near the station, where pH averages 7.97 and conductivity averages  $218.8 \mu\text{S cm}^{-1}$  (Chapman unpublished data). It was periodically aerated to maintain DO levels above  $4 \text{ mg l}^{-1}$ . DO, recorded twice daily, averaged  $5.2 \pm 0.09 \text{ mg l}^{-1}$  (S.E.) in the morning and  $5.6 \pm 0.10 \text{ mg l}^{-1}$  in the afternoon. Water temperature averaged  $18.2 \pm 0.06^\circ\text{C}$  in the morning and  $20.4 \pm 0.06^\circ\text{C}$  in the afternoon.

Following their capture, fish were acclimated to the holding tank conditions for 7 days before they were used in behavioral or oxygen consumption experiments. All behavioral data were collected within 25 days of capture, and all physiological data within 24 days of capture. Fish were fed on a specific daily ration with a 42% protein diet, except 24 h prior to a behavioral or an oxygen consumption trial.

#### *Metabolic rate and critical oxygen tension*

Tolerance to low oxygen may relate in part to the metabolic rate of a fish. Fishes will regulate their metabolic rate over a range of dissolved oxygen concentrations; at some point, though, a further reduction in oxygen tension will produce a shift from a metabolic rate that is independent of oxygen concentration to one that is dependent on it. This point is referred to

as the critical oxygen tension (Beamish 1964, Ultsch et al. 1978). Metabolic rate and critical oxygen tension were measured for males of each species using a closed respirometer. Metabolic rate was determined as routine oxygen consumption (the rate during random movement under experimental conditions) for a range of body sizes of fish held in closed, dark, static chambers (Cech 1990). Metabolic rate measurements were made on 15 specimens of *A. 'wrought-iron'* (six open-water, nine swamp) and eight *A. aeneocolor*. Water volumes in the respirometer chambers ranged from 244 to 526 ml; the average water volume to fish volume ratio was 44:1 to constrain swimming without overly confining and stressing the fish. Fish were starved for 24 h before a trial to minimize effects of digestion and food absorption on oxygen consumption.

The closed respirometry system was designed for use at remote sites without electricity. We placed a single fish in the chamber full of microfiltered river water (to remove biologically active materials) for 1 h prior to the start of a trial. This acclimation period is relatively short compared with some other studies, but the fish were observed to settle down quickly once a trial began. The water in the chamber was aerated with a bubbler during the acclimation period to elevate DO. The chamber was held in a large water-filled cooler in a shaded facility to minimize variation in water temperature during and among runs. Water temperature averaged  $20.1 \pm 0.2^\circ\text{C}$  (S.E.) for *A. 'wrought-iron'* and  $20.2 \pm 0.3^\circ\text{C}$  for *A. aeneocolor*.

At the start of each experiment, the chamber was sealed with an oxygen probe (YSI Model 600) connected to a data collection system; both were run on batteries. The meter was programmed to take measurements of water temperature and DO at 2-min intervals and to display plotted values throughout the trial. Once the critical oxygen tension was detected on the computer-generated plots, the experiment was terminated, and the water in the chamber was quickly returned to normoxia by aeration. Following each trial, the total length and body weight of the fish were recorded, as well as chamber volume. Trial length averaged  $2.36 \pm 0.16 \text{ h}$  (S.E.).

We determined the rate of oxygen consumption ( $\text{mg O}_2 \text{ h}^{-1}$ ) as a function of the partial oxygen pressure ( $\text{PO}_2$ ) in the water. Oxygen consumption rates were calculated for 10-min intervals throughout each trial to select the  $\text{PO}_2$  range over which to estimate routine metabolic rate. The lower end was at least 20 mm Hg higher than the critical oxygen tension ( $P_c$ , which was estimated by eye) to avoid increases in metabolism

near  $P_c$  due to increased gill ventilation rates (Beamish 1964). The upper end excluded any high initial oxygen consumption rates due to higher activity levels at the start of the trial (Cech 1990). We adjusted the observed metabolic rates to 20°C using  $Q_{10}$  values in Winberg (1961) to permit comparison among the samples and species. Analysis of covariance was used to compare total metabolic rates among groups with body weight (total wet weight of specimen) as the covariate. Both variables were  $\log_{10}$  transformed. Adjusted mean total metabolic rates (sample means adjusted for a common mean body weight and a common regression line) and their standard errors were calculated using ANCOVA. There was no significant effect of body weight on  $P_c$  (ANCOVA,  $p > 0.05$ ), so we used t-tests to compare  $P_c$  between swamp and open-water *A. 'wrought-iron'* groups, and between the two *Astatotilapia* species.

#### *Progressive hypoxia*

Many cichlids are known to use aquatic surface respiration (ASR, Kramer & Mehegan 1981) in response to hypoxia, ventilating their gills with water from the air-water interface where diffusion produces a very thin layer of well-oxygenated water (Kramer & McClure 1982, Chapman et al. 1995, Rosenberger & Chapman 2000). Some cichlids move continuously at the surface during ASR, a behavior we refer to as ram-assisted ASR (Chapman et al. 1994, 1995). In addition, some species hold bubbles in their buccal cavities during periods of oxygen stress (Gee & Gee 1991, Chapman et al. 1994, 1995).

In this study we measured the behavioral responses of individual cichlids in a group setting to progressive hypoxia. Each group consisted of five males. We used one group of swamp-dwelling *A. 'wrought-iron'*, four groups of open-water *A. 'wrought-iron'*, and three groups of *A. aeneocolor*. We were unable to return to Lake Kabaleka for additional groups of swamp fish due to rebel activities in the region during the latter part of our field season. For identification, we individually tattooed fish on the posterior lateral muscles with tattoo ink (Rosenberger & Chapman 2000) 2 days prior to their first of three behavioral trials. Groups were held separately in tanks. Because of day-to-day variation in trial conditions due to the field setting, we ran three trials on each group with a minimum of 2 days between successive trials; behavioral data were averaged across trials for all individuals.

For each trial, fish were acclimated for 2.5 h in a 301 (49 × 21 × 29 cm high) Plexiglas aquarium con-

taining filtered river water. To minimize disturbance, we observed fish through a small viewing port in a screen that shielded the aquarium. Every 15 min, we recorded temperature, DO, and the following behavioral variables of individual fish: (a) the percentage of time that a fish used ASR (from 10 measurements per fish, one every 15 sec); (b) the number of gill ventilations of each fish in a 15 sec period; (c) the surface swimming speed during ASR (either forward or backward; number of 10-cm increments traveled in 15 sec); (d) the number of bubbles released from the mouth in a 3-min period during ASR use; and (e) the number of aggressive encounters (e.g., chasing, locking jaws, or quivering that caused another fish to retreat) between fish in a 3-min period.

Following the first set of behavioral observations, we added 2–3 g of sodium sulfite to the water to slowly lower DO (Lewis 1970, Gee & Gee 1991). Lewis (1970) found no observable differences in the behavioral responses of fishes to water freed of oxygen with sodium sulfite and water freed of oxygen by bubbling with nitrogen gas. Once DO decreased below  $0.2 \text{ mg l}^{-1}$ , we waited 30 min before recording the final set of observations (Chapman et al. 1995). Trial length averaged  $5.0 \pm 0.2 \text{ h}$  (S.E.) and water temperature averaged  $19.5 \pm 0.2^\circ\text{C}$  (S.E.). If a fish lost equilibrium during a trial, we quickly removed it and allowed it to recover in normoxic water.

From the ASR-use data, we plotted the percentage of time spent using ASR vs. the  $\text{PO}_2$  of the water for each individual in each trial. We fit a spline curve to these data (using JMP, version 3.1.6.2; with lambda, a stiffness parameter = 10), and determined  $\text{ASR}_{10}$ ,  $\text{ASR}_{50}$ , and  $\text{ASR}_{90}$  thresholds (i.e. the  $\text{PO}_2$  levels at which a fish uses ASR 10%, 50%, or 90% of the time).

Linear regression analyses indicated body size effects on ASR thresholds, with higher ASR levels in smaller fishes. We therefore used analysis of covariance to compare ASR thresholds between groups and species with body weight (wet weight) as the covariate. Both variables were  $\log_{10}$  transformed. Adjusted mean ASR thresholds and their standard errors were calculated using ANCOVA. As individually-marked fish were in group settings, we first tested for group effects on ASR thresholds in the open-water *A. 'wrought-iron'* group and *A. aeneocolor* using ANCOVA. Group effects were not significant for any of the ASR thresholds ( $p > 0.05$ ), so groups were combined to test for interpopulational and interspecific effects.

At high  $\text{PO}_2$ , gill ventilation rates were difficult to quantify because gill ventilation amplitude was

very shallow. We therefore calculated the frequency of gill ventilations for individual fish at low PO<sub>2</sub> (below 25 mm Hg and prior to ASR use, average PO<sub>2</sub> = 17 mm Hg) and during the final sampling interval. We also calculated the drop between the gill ventilation rate prior to ASR and immediately following the initiation of ASR. Aggressive behavior was relatively constant prior to the initiation of ASR for swamp and open-water *A. 'wrought-iron'* and for *A. aeneocolor*. To compare populations and species, we calculated the frequency of aggressive encounters for each individual fish at low PO<sub>2</sub> (pre-ASR, as described for gill ventilations), and compared this to the aggression level during the final sampling interval (>90% ASR). We considered the surface swimming speed (ram-assisted) during ASR and the release rate of buccal bubbles during the final observation interval. We also calculated the loss of equilibrium for each individual over the three trials.

Linear regression analyses indicated body size effects on gill ventilation rates at pre-ASR dissolved oxygen levels, with higher rates in smaller fish. We therefore used ANCOVA to compare gill ventilation rates between populations and species with body weight (wet weight) as the covariate. Both variables were log<sub>10</sub> transformed. As no body size effects were evident for aggression rate, swimming speed during ASR, or bubble holding, we used analysis of variance to compare these other behaviors between populations. Paired t-tests were used to compare gill ventilation rates between the interval prior to ASR and that immediately following the initiation of ASR, as well as aggression between pre-ASR PO<sub>2</sub> levels and the final sampling interval. Based on earlier studies (Chapman et al. 1995, Rosenberger & Chapman 2000), we predicted a significant drop in gill ventilation rate and aggression with the onset of ASR, and therefore used a one-tailed test. Two-tailed tests were used for all other comparisons. We first tested for group effects on all behaviors in the open-water *A. 'wrought-iron'* and *A. aeneocolor*. Only one group effect was detected in one behavioral category at one dissolved oxygen level, so groups were combined to test for interpopulational and interspecific effects.

## Results

### *Metabolic rate and critical oxygen tension*

Analysis of covariance revealed no difference between the metabolic rate-body weight relationships of the

swamp and open-water groups of *A. 'wrought-iron'* (slopes:  $F = 0.477$ ,  $p = 0.507$ ; intercepts:  $F = 0.129$ ,  $p = 0.279$ ), so metabolic rates of the two groups were combined for comparison with *A. aeneocolor*. Similarly, there was no difference in critical oxygen tensions between swamp and open-water *A. 'wrought-iron'* ( $t = 1.147$ ,  $p = 0.276$ ).

Total metabolic rate ranged from 0.30 to 1.17 mg O<sub>2</sub> h<sup>-1</sup> for *A. 'wrought-iron'* (body weight range = 1.94–10.14 g) and 0.51–1.17 mg O<sub>2</sub> h<sup>-1</sup> for *A. aeneocolor* (body weight range = 3.59–7.13 g). There was no difference in adjusted mean total metabolic rate between the two species (*A. 'wrought-iron'* = 0.74 mg O<sub>2</sub> h<sup>-1</sup>; *A. aeneocolor* = 0.82 mg O<sub>2</sub> h<sup>-1</sup>; slopes:  $F = 0.013$ ,  $p = 0.910$ ; intercepts:  $F = 1.602$ ,  $p = 0.220$ , evaluated at a mean body weight of 5.6 g). Similarly, P<sub>c</sub> did not differ between the two species (mean P<sub>c</sub> for *A. 'wrought-iron'* = 13.46 ± 0.71 mm Hg (S.E.); *A. aeneocolor* = 15.00 ± 1.40 mm Hg;  $t = 1.08$ ,  $p = 0.292$ ).

### *Progressive hypoxia*

Both haplochromine cichlid species used aquatic surface respiration when dissolved oxygen became scarce. We found no significant difference in ASR thresholds between *A. 'wrought-iron'* from swamp and open-water sites (ANCOVA adjusted means, ASR<sub>10</sub>:  $F = 0.049$ ,  $p = 0.827$ ; ASR<sub>50</sub>:  $F = 0.108$ ,  $p = 0.747$ ; ASR<sub>90</sub>:  $F = 0.065$ ,  $p = 0.802$ ). Therefore, swamp and open-water fish were combined to test for differences between *A. 'wrought-iron'* and *A. aeneocolor*. ASR<sub>10</sub> thresholds did not differ between the two species (slopes:  $F = 2.043$ ,  $p = 0.163$ ; intercepts:  $F = 0.017$ ,  $p = 0.899$ ), nor did ASR<sub>50</sub> thresholds (slopes:  $F = 0.734$ ,  $p = 0.398$ ; intercepts:  $F = 1.531$ ,  $p = 0.225$ , Figure 2). However, ASR<sub>90</sub> thresholds were lower in *A. 'wrought-iron'* than in *A. aeneocolor* (slopes:  $F = 0.063$ ,  $p = 0.804$ ; intercepts:  $F = 8.297$ ,  $p = 0.007$ ).

Gill ventilation rates at low PO<sub>2</sub> (pre-ASR) were lower in swamp-dwelling *A. 'wrought-iron'* than in *A. aeneocolor* and open-water *A. 'wrought-iron'* (slopes:  $F = 0.056$ ,  $p = 0.817$ ; intercepts:  $F = 18.351$ ,  $p = 0.001$ ). However, there was no difference between swamp and open-water fish during the final sampling interval (slopes:  $F = 0.263$ ,  $p = 0.615$ ; intercepts:  $F = 0.001$ ,  $p = 0.972$ , Table 2). The change in gill ventilation rate with the onset of ASR did not differ between the swamp and open-water groups of *A. 'wrought-iron'* (Mann–Whitney test,  $p = 0.349$ ).

Combined, these *A. 'wrought-iron'* groups showed a significant drop in gill ventilation rate with the onset of ASR (paired  $t = 3.304$ ,  $p = 0.004$ ) in contrast to *A. aeneocolor*, which showed no significant drop (paired  $t = 0.303$ ,  $p = 0.767$ ).

The pre-ASR aggression rate, ram-assisted ASR speed, and bubble-holding frequency differed between

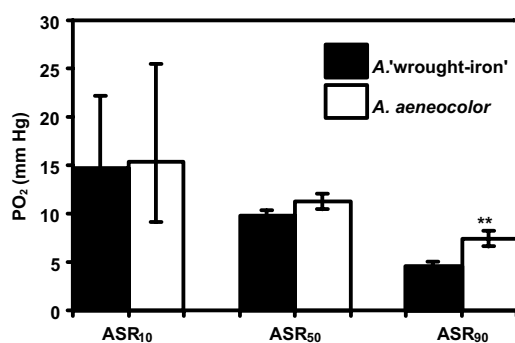


Figure 2. ASR<sub>10</sub>, ASR<sub>50</sub>, and ASR<sub>90</sub> thresholds for two species of haplochromine cichlids from Lake Kabaleka, Uganda (*A. 'wrought-iron'* and *A. aeneocolor*). The values represent antilog adjusted means ( $\pm$ S.E.) calculated from analyses of covariance with log body weight as the covariate.

swamp-dwelling and open-water *A. 'wrought-iron'* groups (t-test,  $p < 0.05$ ), so these groups were treated separately in the following analyses. The pre-ASR aggression rate was higher in swamp-dwelling *A. 'wrought-iron'* than in open-water groups of both species (Table 2). However, the aggression rate dropped in all three groups between the pre-ASR and final intervals (open-water *A. 'wrought-iron'*: paired  $t = 1.856$ ,  $p = 0.043$ ; swamp-dwelling *A. 'wrought-iron'*:  $t = 3.400$ ,  $p = 0.014$ ; *A. aeneocolor*:  $t = 2.033$ ,  $p = 0.033$ ), and did not differ among groups during the final sampling period.

Fish from all three groups swam at the surface during ASR, potentially increasing the amount of well-oxygenated surface film passing over their gills. Ram-assisted ASR speed was higher in *A. 'wrought-iron'* from the swamp than in open-water fish of either *A. 'wrought-iron'* or *A. aeneocolor* (Table 2). A similar pattern was observed for buccal bubble holding; bubble holding was observed in all three groups, but the frequency of bubble exchange was higher in swamp-dwelling *A. 'wrought-iron'* than in open-water fish of either species. Loss of equilibrium was higher in *A. aeneocolor* (28% of the time) than in either swamp-dwelling (0%) or open-water groups of *A. 'wrought-iron'* (6.7%).

Table 2. The behavioral response of *A. aeneocolor*, and open-water and swamp-dwelling *A. 'wrought-iron'* to progressive hypoxia. The pre-ASR data represent average values at low PO<sub>2</sub> prior to the initiation of ASR (mean PO<sub>2</sub> = 17 mm Hg). Post ASR values were calculated for the final sampling interval of the experiment. Adjusted means (derived from ANCOVA,  $\pm$ S.E.) and antilog adjusted means are presented for gill ventilation rate. Means ( $\pm$ S.E.) are presented for all other characters. Groups underlined are not significantly different ( $p < 0.05$ , Scheffe test for ANOVA analyses, and Sidak test for ANCOVA analyses). 1 = *A. 'wrought-iron'* (open-water); 2 = *A. 'wrought-iron'* (swamp); 3 = *A. aeneocolor*.

Behavioral character	<i>A. 'wrought-iron'</i> (open-water) (adj. mean $\pm$ S.E.) [antilog adj. mean]	<i>A. 'wrought-iron'</i> (swamp) (adj. mean $\pm$ S.E.) [antilog adj. mean]	<i>A. aeneocolor</i> (adj. mean $\pm$ S.E.) [antilog adj. mean]	A posteriori comparisons
Gill ventilation rate pre-ASR (# per 15 sec)	1.38 $\pm$ 0.04 [24.21]	1.22 $\pm$ 0.05 [16.52]	1.32 $\pm$ 0.04 [20.89]	<u>1 2 3</u>
Gill ventilation rate post-ASR (# per 15 sec)	1.40 $\pm$ 0.02 [25.00]	1.40 $\pm$ 0.02 [25.35]	1.40 $\pm$ 0.02 [25.35]	<u>1 2 3</u>
Aggression pre-ASR (# attacks per 3 min)	0.84 $\pm$ 0.24	2.67 $\pm$ 0.89	0.73 $\pm$ 0.27	<u>1 2 3</u>
Aggression post-ASR (# attacks per 3 min)	0.26 $\pm$ 0.14	0.33 $\pm$ 0.26	0.13 $\pm$ 0.09	<u>1 2 3</u>
Bubble holding (# releases in 3 min)	1.87 $\pm$ 0.17	2.60 $\pm$ 0.13	1.21 $\pm$ 0.25	<u>1 2 3</u>
Ram-assisted ASR speed (cm per 15 sec)	31.89 $\pm$ 6.30	63.33 $\pm$ 5.06	21.43 $\pm$ 7.04	<u>1 2 3</u>

## Discussion

### *Interpopulational variation*

Papyrus dominates much of the 85 000 km<sup>2</sup> of permanent swamp that occurs on the African continent (Beadle & Lind 1960, Beadle 1981, Thompson & Hamilton 1983). The oxygen-scarce conditions that characterize the dense interior of papyrus can limit habitat use and dispersal of non-air-breathing fishes (Chapman et al. 1999). For fishes that cannot tolerate low oxygen conditions, dense swamps may serve as a barrier to dispersal and potentially lead to diversification. For non-air breathers that can survive in dense wetlands, their use of these habitats is still likely to be limited by the spatial and temporal patterns of variation in oxygen content within the wetland and the efficiency of oxygen uptake in the species. This may lead to geographical variation between populations in wetland and open-water habitats.

Within Lake Kabaleka, we found that open-water and swamp-dwelling *A. 'wrought-iron'* differed in some aspects of their respiratory behavior. Swamp-dwelling fish showed lower gill ventilation rates prior to the initiation of ASR, higher pre-ASR aggression rates, higher swimming speed during aquatic surface respiration, and a higher rate of bubble release than both the open-water group of *A. 'wrought-iron'* and *A. aeneocolor*. The lower gill ventilation rate prior to ASR use (at an average PO<sub>2</sub> of 17 mm Hg) suggests either a lower activity level or a greater oxygen uptake capacity, more likely the latter since the activity of swamp fish was greater due to higher rates of aggression. Active swimming during ASR (ram-assisted ASR) may also increase the efficiency of oxygen uptake during ASR by forcing oxygenated water over the gills (Chapman et al. 1994). Even swimming backwards, although it does not force water over the gills, does allow the fish to exploit a new, oxygenated surface film (Chapman et al. 1995). Greater oxygen delivery associated with greater surface swimming speed may increase hypoxia tolerance, providing that energy expended for faster swimming does not exceed the benefits of exposure to more surface film. Buccal-bubble holding may also increase ASR efficiency. This behavior has been advocated as a buoyancy compensation mechanism for negatively buoyant fish (Gee & Gee 1991) and also as a mechanism to increase the oxygen content of the water passing over the bubble (Burggren 1982, Kramer 1983a). The higher frequency of bubble exchange in the swamp-dwelling fish may increase oxygen-uptake efficiency

by maintaining a high diffusion gradient between the air bubble and intake water.

The differences in ASR behavior between the swamp and open-water fish may reflect interpopulational variation in selection pressure for low-oxygen tolerance between swamp and open-water habitats. Previous studies on other African fishes have revealed variation among swamp and open-water populations that relate to differences in oxygen content among sites. For example, total gill surface area is larger in swamp-dwelling populations of the mormyrid, *Gnathonemus victoriae*, and the haplochromine cichlid, *Pseudocrenilabrus multicolor victoriae*, than in populations of the same species from well-oxygenated sites (Chapman et al. 2000, Chapman & Hulen 2001). In addition, a suite of studies has demonstrated small-scale geographical variation in gill morphology, respiratory behavior, and respiratory physiology among populations of the African cyprinid *Barbus neumayeri* that correlates with dissolved oxygen availability (Chapman & Liem 1995, Olowo & Chapman 1996, Chapman et al. 1999, L. Chapman unpublished data). Whether this variation in respiratory behaviors between swamp and open-water fishes represents genetic variation, phenotypic variation, and/or their interaction is largely unknown. However, Chapman et al. (1999) did find genetic differences between swamp and open-water populations of *Barbus neumayeri* that may reflect habitat-specific selection pressures. Thus, papyrus swamps may contribute to the diversification of populations through strong selection for tolerance of the extreme physico-chemical conditions that characterize the dense swamp interior, an effect that may be particularly poignant in site-tenacious taxa.

### *Interspecific variation*

Several lines of evidence suggest that *A. 'wrought-iron'* is more hypoxia tolerant than *A. aeneocolor*. These include a lower ASR<sub>90</sub> threshold, a drop in gill ventilation rate with the onset of ASR, and a lower loss of equilibrium under extreme hypoxia. Aquatic surface respiration is a widespread behavior among non-air-breathing fishes that inhabit hypoxic waters (Gee et al. 1978, Kramer & McClure 1982, Kramer 1983a,b, Winemiller 1989, Chapman et al. 1994, 1995, Chapman & Chapman 1998). However, there are certain costs that may result in selection to increase ASR efficiency and decrease ASR thresholds. Increased time at the surface may be energetically expensive, limit



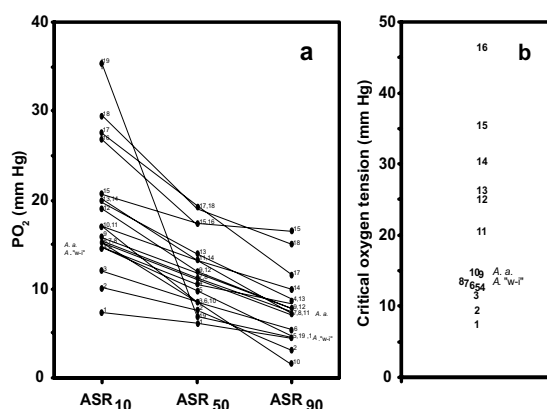


Figure 3. a – ASR<sub>10</sub>, ASR<sub>50</sub>, and ASR<sub>90</sub> thresholds (mm Hg) and b – critical oxygen tension (mm Hg) for several species of East African cichlids. A. ‘wrought-iron’ (A. w-i) and *A. aeneocolor* (A. a.) are highlighted on the figure. For (a) the numbers represent the following species: 1 – *Oreochromis esculentus* (open-water, L. Victoria), 2 – *Neochromis nigricans* (open-water, L. Victoria), 3 – *Cyprichromis leptosoma* (open-water, L. Tanganyika), 4 – *H. ‘rock-kribensis’* (open-water, L. Victoria), 5 – A. ‘wrought-iron’ (open-water & swamp-dwelling, L. Kabaleka), 6 – *Pseudocrenilabrus multicolor victoriae* (swamp-dwelling, L. Nabugabo), 7 – *Prognathochromis perrieri* (open-water, L. Victoria), 8 – *A. aeneocolor* (open-water, L. Kabaleka), 9 – *Enterochromis ‘firetruck’* (open-water, L. Saka), 10 – *Labrochromis ishmaeli* (open-water, L. Victoria), 11 – *Pyxichromis orthostoma* (open-water, L. Victoria), 12 – *Enterochromis ‘rainbow’* (open-water, L. Saka), 13 – *Prognathochromis venator* (open-water, L. Victoria), 14 – *Astatoreochromis alluaudi* (L. Victoria), 15 – *Yssichromis argens* (open-water, L. Victoria), 16 – *Neolamprologis tretocephalus* (open-water, L. Tanganyika), 17 – *Astatotilapia velifer* (open-water ecotone, L. Nabugabo), 18 – *Tropheus moorii* (open-water, L. Tanganyika), 19 – *Oreochromis niloticus* (L. Victoria). ASR data were abridged from Chapman et al. (1995) for 1–4, 7, 10–11, 15–16, 18–19; Melnychuk (1999) for 9, 12; and Rosenberger & Chapman (2000) for 6, 13, 17. For (b) the numbers represent the following species: 1 – *Pseudocrenilabrus multicolor victoriae* (swamp-dwelling, L. Nabugabo), 2 – *Astatoreochromis alluaudi* (swamp-dwelling, L. Nabugabo), 3 – *Prognathochromis venator* (open-water, L. Kyanja), 4 – *Oreochromis leucostictus* (swamp-dwelling, L. Nabugabo), 5 – *Astatoreochromis alluaudi* (open-water, Mpanga R.), 6 – *Astatotilapia velifer* (swamp ecotone, L. Nabugabo), 7 – *Pseudocrenilabrus multicolor victoriae* (open-water, Mpanga R.), 8 – A. ‘wrought-iron’ (open-water & swamp, L. Kabaleka), 9 – *Enterochromis ‘rainbow’* (open-water, L. Saka), 10 – *A. aeneocolor* (open-water, L. Kabaleka), 11 – *Enterochromis ‘firetruck’* (open-water, L. Saka), 12 – *Astatotilapia burtoni* (open-water, L. Tanganyika), 13 – *Melanochromis auratus* (open-water, L. Malawi), 14 – *Oreochromis niloticus* (L. Victoria), 15 – *Dimidiochromis compressiceps* (open-water, L. Malawi), 16 – *Tropheus moorii* (L. Tanganyika). Data were abridged from Verheyen et al. (1994) for 12–16; Melnychuk (1999) for 9, 11; Rosenberger & Chapman (2000) for 1, 3, 6; and Chapman & Chapman

the time available for other activities, and increase risk of predation (Kramer et al. 1983, Kramer 1987). The lower ASR<sub>90</sub> threshold in A. ‘wrought-iron’ suggests that other respiratory mechanisms may differ between the species and compensate for less frequent ASR use, permitting fish to spend less time at the surface under extreme hypoxia. The ASR thresholds for A. ‘wrought-iron’ fall into the lower third of the range of values reported for other East African cichlids (Figure 3a). *A. aeneocolor* seems to fall in the lower range for ASR<sub>10</sub> but the middle range for ASR<sub>90</sub>.

The gill ventilation rate in A. ‘wrought-iron’ decreased between the pre-ASR level and the onset of ASR. If a decline in gill ventilation rate indicates enhancement of oxygen uptake, this decrease demonstrates higher oxygen uptake efficiency in A. ‘wrought-iron’ than in *A. aeneocolor*. Based on loss of equilibrium data, Chapman et al. (1995) concluded that three Lake Tanganyikan cichlids were less tolerant of hypoxia than ecologically similar cichlid species from the lower-oxygenated Lake Victoria. They also found no decline in gill ventilation rate with the initiation of ASR for the three Lake Tanganyikan cichlids, but a marked decline for the Lake Victoria species.

The resting routine metabolic rate and critical oxygen tension did not differ between swamp-dwelling and open-water A. ‘wrought-iron’, or between A. ‘wrought-iron’ and *A. aeneocolor*. Both species exhibit a critical oxygen tension falling within the lower range for East African cichlids; however, several species have lower tensions than the Kabaleka cichlids (Figure 3b). Of the 16 species of East African cichlids considered, seven species exhibit a critical oxygen tension lower than A. ‘wrought-iron’, and 9 species exhibit a tension lower than *A. aeneocolor*. The two East African cichlids that exhibit the lowest critical tensions are widely distributed species that frequently occur in dense swamps (*Astatoreochromis alluaudi* and *Pseudocrenilabrus multicolor victoriae*).

Our comparative data on A. ‘wrought-iron’ and *A. aeneocolor* indicate the value of hypoxia tolerance data as a predictor of fish distribution. *A. aeneocolor* does occur in the fringing wetland of Lake Kabaleka, but at a much lower density than A. ‘wrought-iron’, which may reflect a lower tolerance to the extreme

(unpublished data) for 2, 4, 5, 7. The protocol for determining ASR thresholds was very similar among studies; all looked at response to progressive hypoxia over a similar time frame. Critical tensions for all studies were estimated using closed respirometry.

hypoxia that characterizes the dense swamp interior. Other studies have noted the importance of hypoxia tolerance as a predictor of fish distribution and community structure in dense African swamps (Chapman et al. 1996a,b, 1999, Rosenberger & Chapman 1999, 2000) and temperate lakes (Tonn & Magnuson 1982, Rahel & Nutzman 1994). In the Lake Victoria basin, hypoxia tolerance has also been important in determining persistence in wetland refugia, habitats where indigenous species may be protected from predation by the introduced, but hypoxia-intolerant Nile perch (Chapman et al. 1996a,b, Chapman & Chapman 1998, Schofield & Chapman 1999, 2000, Rosenberger & Chapman 2000).

#### *Implications for interlacustrine dispersal*

Patterns of hypoxia tolerance among haplochromine cichlid species and lineages may contribute to our understanding of interlacustrine transfer. Hydrographic systems in the Lake Victoria basin are temporally labile, characterized by fluctuating water levels (Coulter 1994). During flood periods, dissolved oxygen levels in wetlands and swampy channels usually rise, relaxing hypoxic barriers and potentially permitting passage to hypoxia-intolerant species (Chapman & Liem 1995, Kaufman et al. 1997, Chapman et al. 1998). Conversely, hypoxia-tolerant species should be continually able to persist in wetlands and pass through swampy corridors even during low flood conditions, unless they dry up completely (Chapman & Liem 1995).

We know that cichlid species show a wide range of hypoxia tolerance (Figure 3). The potential for invasion and subsequent adaptive radiation in newly-forming lakes may depend upon changes in water level and differences in hypoxia tolerance among taxa. At one extreme are highly tolerant species, such as the haplochromine cichlid *Pseudocrenilabrus multicolor victoriae* and *A. alluaudi* that are widespread in lakes, rivers, and swamp corridors of the greater Lake Victoria region (Lowe-McConnell 1991, Chapman et al. 1996a,b, Kaufman 1997). Fishes of intermediate tolerance may be just able to penetrate a few kilometers into dense swamps, such as *A. 'wrought-iron'* and *A. aeneocolor* in the Lake Kabaleka swamp. *A. aeneocolor* is rare, while *A. 'wrought-iron'* occurs at a higher density, but both are there. Dissolved oxygen in the swamp channel is very low ( $1.57 \text{ mg l}^{-1}$  in the surface waters), but certainly not as low as

other dense swamps of the Lake Victoria region (Chapman & Liem 1995, Chapman & Chapman 1998, Chapman et al. 1998, 2001), which may permit the level of penetration that we observed. It is likely that dissolved oxygen levels in this corridor decrease as the open channel grades into dense papyrus. Future expeditions that penetrate the corridor beyond 1500 m will be important to our understanding of haplochromine dispersal in this system. Nevertheless, our study suggests that some generalized lacustrine haplochromines may 'leak' through swamp corridors even under relatively extreme conditions. Kaufman et al. (1997) noted other lines of evidence for haplochromine cichlid dispersal between lakes including: the fact that extant Lake Victoria haplochromines have congeners in the Lake George-Edward system, the presence of lacustrine haplochromines in the Victoria Nile, and the presence of species common to both lakes Edward and George in the adjoining Kazinga Channel.

Swamp leakage may be an important mechanism for interlacustrine dispersal in the Lake Victoria basin, particularly during major flood cycles that may modulate the extreme conditions in the swamp channels. Our comparative data on the ASR thresholds and critical oxygen tensions of the *Astatotilapia* species from Lake Kabaleka suggest intermediate tolerance (Figure 3) and the ability to penetrate the swamp corridor separating Lakes Kabaleka and George. *A. aeneocolor* was first described from Lake George, and interlacustrine transfer may have occurred under favorable flood conditions. Whether this species is the antecedent of the two potentially endemic haplochromines in the system is unknown, but future genetic studies will help to address this issue.

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