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# The distribution and feeding ecology of the characid *Brycinus sadleri* in Lake Nabugabo, Uganda: implications for persistence with Nile perch (*Lates niloticus*)

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Coincident with a rapid increase in numbers of introduced predatory Nile perch (*Lates niloticus*) in lakes Victoria, Kyoga, and Nabugabo of east Africa was a dramatic decline in populations of many native fishes. However, a few species, including the characid *Brycinus sadleri*, have shown remarkable resilience. This study examined how the distribution and foraging behaviour of *B. sadleri* in Lake Nabugabo may facilitate their persistence with Nile perch. Both *B. sadleri* and Nile perch were most abundant in exposed areas offshore (20m) as opposed to wetland areas. However, we found evidence for a strong diel shift in activity and modest changes in the habitat use of *B. sadleri* that may contribute to persistence with Nile perch. In general, *B. sadleri* actively foraged during the daylight hours and remained quiet during the night. Nile perch began foraging during the early evening and were more active during the night than during the day. By early morning the proportion of full stomachs in Nile perch was low, though there was evidence of a low level of feeding activity during the day. Stomach contents of *Brycinus sadleri* indicated a shift from surface to benthic feeding as light levels increased, which appears to decrease their susceptibility to predation by Nile perch during the daylight hours.

**Keywords:** African fishes, diel activity, Lake Victoria basin, non-indigenous species

## Introduction

One strategy commonly employed to manage collapsing fisheries is the introduction of non-native species to replace devastated fish stocks (Welcomme 1981, 2003). Although fish introductions may indeed be useful in increasing yield, they can also have many negative impacts, including predation on indigenous species, introduction of parasites, competition with indigenous species, hybridisation, and the alteration of food webs (Welcomme 1984, Achieng 1990, Ogutu-Ohwayo 1990a, Witte *et al.* 1992). Nowhere is this better exemplified than in the Lake Victoria basin of east Africa.

In the late 1950s and early 1960s, the predatory Nile perch (*Lates niloticus*) and four tilapiine species (*Oreochromis niloticus*, *O. leucostictus*, *Tilapia zillii* and *T. rendalli*) were introduced into Lake Victoria in an effort to increase depleted fisheries and, in the case of Nile perch, also to improve the game fishery (Fryer 1960, Ogutu-Ohwayo 1990a, 1990b, 1993, 1994, Jackson 2000). The Nile perch is a large centrromid fish that can reach over 2m in length and exhibits an ontogenetic dietary shift from invertebrate feeding to piscivory (Ogutu-Ohwayo 1993, 1994, Schofield and Chapman 1999). In Lake Victoria, by the 1960s catches of many species had declined, and others declined in the 1970s, due most probably to intense

exploitation (Balirwa *et al.* 2003). However, the dramatic increase in Nile perch that occurred in the 1980s coincided with a further decline in the populations of several native species (Barel *et al.* 1985, Kaufman 1992, Witte *et al.* 1992, Balirwa *et al.* 2003). Most notably, over 50% of the non-littoral haplochromines, comprising about 40% of the endemic haplochromine cichlid assemblage, in Lake Victoria disappeared (Kaufman 1992, Witte *et al.* 1992, Seehausen *et al.* 1997a, 1997b). Predation by the Nile perch is thought to have been a major cause of this faunal collapse, although other factors, such as eutrophication and deoxygenation of the deeper waters of the lake (Hecky 1993, Hecky *et al.* 1994), may also have played a role (Kaufman and Ochumba 1993, Seehausen *et al.* 1997a, Balirwa *et al.* 2003). Similar changes occurred with the introduction of Nile perch into other lakes in the basin, including Lake Kyoga (Ogutu-Ohwayo 1994), central Ugandan satellite lakes (Kaufman *et al.* 1997) and Lake Nabugabo (Ogutu-Ohwayo 1993, Chapman *et al.* 1996a, 1996b).

Despite dramatic declines in the populations of many native fishes, some species have persisted with Nile perch. Satellite water bodies around the main lakes harbor small remnant faunas of the larger lakes (Ogutu-Ohwayo 1993,

Kaufman *et al.* 1997). Within Lake Victoria, rocky shores and rocky islands are important refugia because of their high structural complexity and clearer waters, which facilitate coexistence of many fishes (Seehausen 1996, 1999, Seehausen *et al.* 1997b). Wetlands also protect some fishes from predation by Nile perch because they provide both structural and low oxygen refugia for prey species and serve as barriers to the dispersal of Nile perch (Chapman *et al.* 1996a, 1996b, Rosenberger and Chapman 1999, 2000, Schofield and Chapman 1999, 2000). In addition, there are some species that have persisted with Nile perch in the absence of structural refugia including the cyprinid *Rastrineobola argentea* and the characid *Brycinus sadleri*. *Rastrineobola argentea* is abundant in the open waters of lakes Victoria, Kyoga and Nabugabo, and has comprised a major part of the prey of the introduced Nile perch (Ogutu-Ohwayo 1990a, 1990b, 1993, 1994). Interestingly, the catch rate of *R. argentea* has shown a dramatic increase since the introduction of Nile perch, which has been attributed to the relaxation of competitive pressure by haplochromines subsequent to the Nile perch boom (Wanink and Witte 2000). *Rastrineobola argentea* is active in the open waters at night, when Nile perch are also active (Wanink 1998). The overlap in both the time and area of activity between *R. argentea* and Nile perch, and the fact that *R. argentea* is very abundant, may account for a high level of predation on this species. *Brycinus sadleri*, on the other hand, is found mainly in littoral areas of the lakes and appears not to be preyed upon by Nile perch. For example, in Lake Victoria (1988–1992) Ogutu-Ohwayo (1994) found no *B. sadleri* in the stomachs of 5 455 Nile perch (<20cm to >100cm in total length). Ogutu-Ohwayo (1994) examined stomachs of 826 Nile perch of a similar size range (1991 and 1993) in Lake Nabugabo, and recovered only one specimen of *B. sadleri*. The absence of predation by Nile perch on *B. sadleri* suggests minimal overlap between the two species. However, the diel distribution and feeding ecology of *B. sadleri* remains largely unknown.

Species that have persisted with Nile perch are extremely important because they are the seeds for resurgence, should predator pressure be reduced and/or should environmental conditions facilitate resurgence. In some lakes of the Lake Victoria basin and in some sections of Lake Victoria, resurgence of some indigenous species has already occurred (Seehausen *et al.* 1997b, Witte *et al.* 2000, Chapman *et al.* 2003, Balirwa *et al.* 2003), and seems to have coincided with intense fishing that has reduced numbers of large Nile perch (Balirwa *et al.* 2003). Species like *Brycinus sadleri*, which have not shown an apparent decline in the presence of Nile perch, now face an increasing abundance of potential competitors in littoral and open waters as species that were confined to structural refugia resurge. An understanding of characters that facilitate persistence with Nile perch and the ecology of persisting species is critical to predicting the future of fish communities in these dynamic systems.

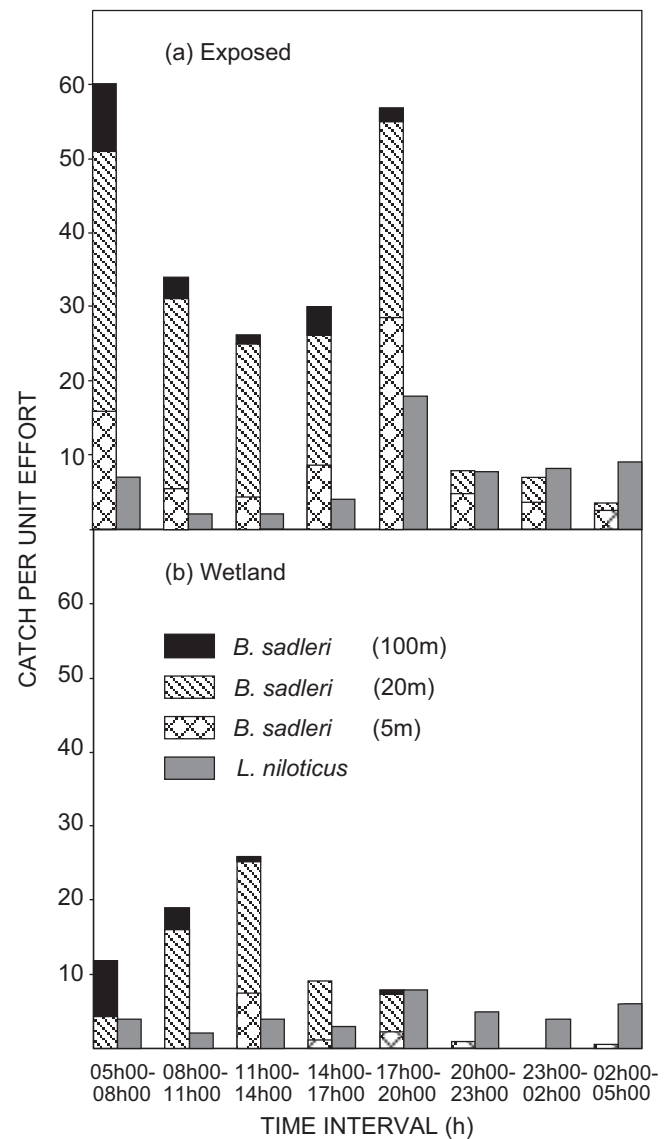
The objective of this study was to quantify the distribution and feeding ecology in Lake Nabugabo of *B. sadleri*, a non-cichlid that has persisted with Nile perch, so as to identify characteristics of the species that may have permitted

resilience to Nile perch invasion. This objective was achieved by: a) quantifying the distribution of *B. sadleri* in the lake relative to Nile perch and b) examining the diel pattern of feeding and activity of *B. sadleri* relative to Nile perch to assess the role of diel activity patterns in minimising exposure to Nile perch predation.

## Materials and methods

### Study site

Lake Nabugabo is a small satellite lake (24km<sup>2</sup>, mean depth = 4.5m) that lies just south of the equator in Uganda. The



**Figure 1:** Average abundance (catch per unit effort, CPUE) of *Brycinus sadleri* and Nile perch (*Lates niloticus*) over the diel cycle in Lake Nabugabo, Uganda, for a) exposed and b) wetland habitats in 1995. Each bar represents the average catch for the four sampling periods. For *B. sadleri*, CPUE are indicated for fish collected 5m, 20m, and 100m offshore

lake was isolated from Lake Victoria approximately 4 000 years ago (Beadle 1962, Greenwood 1965, see Figure 1 in Schofield and Chapman 1999) and lies within the extensive Lwamunda Swamp that was formerly a bay on the western shore of Lake Victoria (Worthington 1932, Greenwood 1965, Ogutu-Ohwayo 1993). The lake margin is primarily swamp dominated by hippo grass (*Vossia cuspidata*), *Miscanthidium violaceum*, and water lilies (*Nymphaea lotus* and *N. caerulea*), with small stands of papyrus (*Cyperus papyrus*). On the western side, there are some non-wetland ecotones including swamp forest, rock cliffs, and grass margins. Structural complexity in the swamp forest and rock cliff areas is present in the form of deadfall, overhanging vegetation, and marginally flooded forest.

Nile perch were introduced into Lake Nabugabo in 1960 and 1963 (Ogutu-Ohwayo 1993). A 1962 Cambridge expedition recorded 30 fish species in Lake Nabugabo, including 20 non-cichlids, eight haplochromine cichlids (five endemic to Nabugabo and nearby small lakes), and two tilapiines (Cambridge Nabugabo Biological Survey (CNBS) 1962, Greenwood 1965). Although 119 Nile perch were introduced prior to the Cambridge expedition, none were recorded in their survey (CNBS 1962). The fishery at that time was dominated (by mass) by lungfish (*Protopterus aethiopicus*), followed by *Bagrus docmac*, *Schilbe intermedius*, *Clarias gariepinus*, *Oreochromis esculentus*, *O. variabilis*, and various species of haplochromine cichlids. A survey conducted by Ogutu-Ohwayo (1993) in 1991 and 1992, 30 years after introduction of Nile perch and non-indigenous tilapiines, showed a dramatic change in the fish assemblage. Of the species that formed the basis of the fishery prior to the establishment of Nile perch, *O. esculentus*, *O. variabilis* and *B. docmac* were extirpated, and *S. intermedius*, *C. gariepinus* and *P. aethiopicus* were rare. Nile perch (introduced), Nile tilapia (introduced), *S. intermedius*, *B. sadleri* and *R. argentea* dominated the open waters of the lake (Ogutu-Ohwayo 1993).

### Fish distribution

Habitat use by *Brycinus sadleri* was studied on the western side of the lake. Approximately 50% of this area is bordered by wetland and the remainder is bordered by forest, rock cliffs, and grass landings, which we refer to as 'exposed' habitat. The study area was divided into 200m sections (transects) along the shoreline. Ten of a total of 46 demarcated transects were randomly selected from each of the two habitats, and these were sampled between May and July 1995.

At the time of the study, fishermen at Lake Nabugabo reported reduced catches of Nile perch, presumably associated with intense fishing of the stock. To detect inter-annual changes in the relative abundance of Nile perch, and any concomitant changes in the abundance of *B. sadleri*, 10 of the 20 transects (5 wetland and 5 exposed) were resampled in June and July of 1996 and 1997. Each transect was sampled inshore and offshore using a combination of minnow traps and experimental gill nets to capture most fish species as well as a range of sizes. Ten metal minnow traps were set at 5m intervals along the shoreline. Two multi-mesh gill nets, each 30m long, 1.9m in depth, and comprising four panels

of 25.4mm, 50.8mm, 76.2mm, and 101.6mm stretched mesh, were set parallel to the shoreline approximately 5m and 20m from the shore. Float and lead lines maintained open nets. A minnow trap and anchor were set at each end of both nets. The nets and traps were set in the morning and retrieved the following morning. A YSI oxygen meter (model 50B or 51B) was used to measure dissolved oxygen (mg l<sup>-1</sup>) and water temperature (°C) at each trap and at the top and bottom of the ends of the nets. Fish were measured and identified to the lowest taxonomic category possible in the field.

For the extensive field sampling period (1995), a t-test was used to detect differences in mean dissolved oxygen concentration and water temperature between wetland and exposed transects at the ecotone, and at 5m and 20m offshore. Surface and bottom values were combined for each net. Habitat use by *B. sadleri* and Nile perch were compared for the 20 transects sampled in 1995 using two analyses. First, we calculated the overall abundance of *B. sadleri* and Nile perch in wetland and exposed areas for all gears combined and compared the mean values for the two habitats using a t-test on log<sub>10</sub> transformed data. Second, using only gill net data, we used a split-plot two-way ANOVA to examine the effects of habitat and distance from shore on the catch per unit effort of *B. sadleri* and Nile perch. Data from 1995, 1996, and 1997 were then used to examine inter-annual shifts in the relative abundance of *B. sadleri* and Nile perch using a repeated-measures ANOVA. Following Potvin *et al.* (1990), Mauchly's criterion was used to test for the compound symmetry of the variance-covariance matrix.

### Diel samples and stomach contents analysis

Diel sampling was carried out in June 1995. One wetland and one exposed area were selected to examine diel activity patterns of *B. sadleri* and Nile perch. Each major habitat type was sampled on four occasions, with a minimum of seven days between samples from the same habitat type. At each site three experimental gill nets were set, with one net at 5m, 20m and 100m from the shore. Nets were staggered so that fish moving offshore or onshore were not all captured in the first net. Water depths averaged 0.6m, 2m and 3m at the nets set at approximately 5m, 20m and 100m offshore, respectively. Nets were checked at 3h intervals over a 24h period and the number of both target species and the size of each fish captured were recorded. These data were used to produce estimates of catch per unit effort for *B. sadleri* and Nile perch over the 24h cycle.

During diel sampling, up to 20 *B. sadleri* were collected during each 3h sampling period to determine diel patterns of foraging. Stomach contents were sorted into prey categories, and prey types were identified to the level of family or genus where possible. The percentage mass (i.e. mass of a food category divided by the total food mass for all stomachs x 100) was determined for each stomach. In addition, the frequency of occurrence (the number of fish containing a given prey type ÷ the total number of fish containing food x 100), and the number of individuals of each prey type in each stomach were determined. From the above parameters the 'absolute importance index' (AI), and the 'relative importance index' (RI) were calculated for each fish accord-

ing to the method of George and Hadley (1979) as follows:

AI = % frequency of occurrence + % total numbers + % total mass,

$$RI = 100 AI \sum_{i=1}^n AI$$

where  $n$  is the number of different food types in each time period.

The chi-squared test of independence was used to examine whether the frequency of occurrence of different food categories was independent of time of day. Changes in the composition of the stomach contents over a diel cycle were also analysed using Horn's modification of Morisita's index of niche overlap (Krebs 1989, Finuncane *et al.* 1990):

$$C_H = \frac{2 \sum P_{ij} P_{ik}}{\sum P_{ij}^2 + \sum P_{ik}^2}$$

where  $C_H$  is Morisita's index of overlap between the stomach contents of fish caught at time intervals  $j$  and  $k$ , respectively;  $P_{ij}$  and  $P_{ik}$  are the proportions of prey type  $i$  consumed by fish from the two time intervals. The indices were calculated using RI values for the gut contents of fish caught at various time intervals in the exposed and wetland habitats. In addition, the numbers of individuals of different prey items and their weights were tabulated to provide alternative methods of evaluating the changes in prey composition and feeding intensity over the diel period. Prey types were identified to family or genus level where possible. For all fish with stomach contents, the total number of individual prey and the total mass of the prey were calculated and used to determine average values for a time period. Fullness of the stomachs was determined using a 4-point scale. Only stomachs rated as completely full (4) were used in our comparison of empty and full stomachs over the diel cycle.

During the third week of diel sampling beach seining was carried out twice within 100m of the shore, using a 25mm (stretched mesh) seine, to examine in more detail the diel feeding activity of Nile perch. Beach seining provided larger samples of Nile perch of a larger size range than did the gill nets. Seining was done at 2h intervals along an exposed sandy beach, and stomach contents analysis of Nile perch

was carried out in the field. To determine the intensity of feeding of Nile perch during a 24h period, again the fullness of the stomachs was estimated. Data on activity and feeding of *B. sadleri* were compared to the Nile perch data. A Chi-squared test of independence was used to examine whether the proportion of full and empty stomachs of Nile perch were independent of the time of day. The average values from two sets of beach seine samples were used for this analysis.

## Results

### Dissolved oxygen

Dissolved oxygen (DO) concentrations were higher in the exposed transects than in the wetland transects for measurements taken in the ecotonal region (next to marginal vegetation or as close to the shore as possible); (exposed: mean DO =  $4.8 \pm 0.9$ mg l<sup>-1</sup>, SD; wetland: mean DO =  $2.5 \pm 1.3$ mg l<sup>-1</sup>,  $t = 4.76$ ,  $P < 0.001$ ), for measurements taken 5m offshore (exposed: mean DO =  $4.6 \pm 0.9$ mg l<sup>-1</sup>; wetland: mean DO =  $2.7 \pm 1.2$ mg l<sup>-1</sup>,  $t = 4.25$ ,  $P < 0.001$ ), and for values at the 20m offshore sites (exposed: mean DO =  $4.8 \pm 0.9$ mg l<sup>-1</sup>; wetland: DO =  $3.5 \pm 1.2$ mg l<sup>-1</sup>,  $t = 2.69$ ,  $P = 0.015$ ). Water temperature did not differ between wetland and exposed habitats ( $P > 0.36$ ), averaging 23.7°C in wetland transects and 24.0°C in exposed transects.

### Fish distribution and abundance

In the habitat-wide survey (1995), *B. sadleri* were more abundant in exposed habitats (antilogged mean number of *B. sadleri* per transect: 85.3, range = 11–520) than in the wetland habitats (antilogged mean number per transect: 25.5, range = 3–367,  $t = 2.18$ ,  $P = 0.043$ ). Nile perch showed a similar pattern of abundance to that of *B. sadleri*, with greater abundance in the exposed transects ( $t = 2.86$ ,  $P = 0.010$ ). The antilogged mean number of Nile perch was 16.9 in the exposed transects (range = 6–39) and 8.0 in the wetland transects (range = 3–15).

To examine the significance of distance from shore, habitat type, and their interaction on the CPUE of *B. sadleri* and Nile perch, we used inshore and offshore gill net data from exposed and wetland areas. Habitat and distance from shore were significant factors affecting *B. sadleri* abundance; however, there was no significant interaction

**Table 1:** Two-way split-plot analysis of variance showing the effects of habitat (wetland vs exposed), distance (inshore vs offshore), and their interaction (habitat x distance) on the abundance of *Brycinus sadleri* and *Lates niloticus* in Lake Nabugabo, Uganda (May–July 1995)

<i>Brycinus sadleri</i>				
Source of variation	df	MS	F	P
Habitat	1	2.712	5.156	0.036
Distance	1	4.409	15.857	0.001
Habitat x distance	1	0.004	0.149	0.704
Error	18	0.278		
<i>Lates niloticus</i>				
Source of variation	df	MS	F	P
Habitat	1	308.03	10.35	0.005
Distance	1	156.03	10.93	0.004
Habitat x distance	1	75.63	5.30	0.033
Error	18	14.27		

between habitat and distance (Table 1). *Brycinus sadleri* were more abundant in areas 20m offshore than in inshore areas and more abundant in exposed habitats than in wetland habitats. For Nile perch, habitat, distance and their interaction were all significant factors affecting CPUE (Table 1). Nile perch were most abundant in the offshore areas of exposed transects; in wetland areas, they were low in abundance, and there was no difference between inshore and offshore nets.

Although there seemed to be a declining trend in the CPUE of *B. sadleri* between 1995 and 1997 (mean CPUE = 92.3 fish per transect, 52.2 fish per transect, and 35.9 fish per transect for 1995, 1996 and 1997, respectively), a repeated measures analysis of variance indicated no significant change among years ( $F = 1.689$ ,  $P = 0.216$ ). Similarly, Nile perch in transects sampled between 1995 and 1997 showed no significant change in CPUE ( $F = 1.577$ ,  $P = 0.237$ ).

### Diel samples

Plots of abundance versus time of day for *B. sadleri* during each sampling period showed clear diel patterns. The numbers of *B. sadleri* caught at different time intervals were therefore averaged for the four different sampling periods for each habitat. In both wetland and exposed habitats, the catch per unit effort of *B. sadleri* was much higher during the

day than during the night (Figure 1). In the exposed habitat, where *B. sadleri* were most abundant, activity peaks were recorded between 05h00 and 08h00 and between 17h00 and 20h00. In the wetland habitat, where *B. sadleri* was far less abundant, CPUE was highest between 11h00 and 14h00 with no crepuscular peaks (Figure 1). Most specimens of *B. sadleri* were captured at 20m offshore in both the wetland and exposed habitat (exposed: mean per time interval = 16.9, range = 0.3–35.3; wetland: mean = 5.8, range = 0–18, Figure 1). Very few fish were captured at 100m offshore (exposed: mean per time interval = 2.2, range = 0–9.8; wetland: mean = 1.6, range = 0–8.8), and those that were captured were caught primarily between 05h00 and 08h00 (Figure 1). The inshore net set approximately 5m from shore captured an intermediate number of *B. sadleri* (exposed: mean per time interval = 8.8, range = 2–28; wetland: mean = 1.4, range = 0–7.5), and most fish were captured between 17h00 and 20h00 (Figure 1).

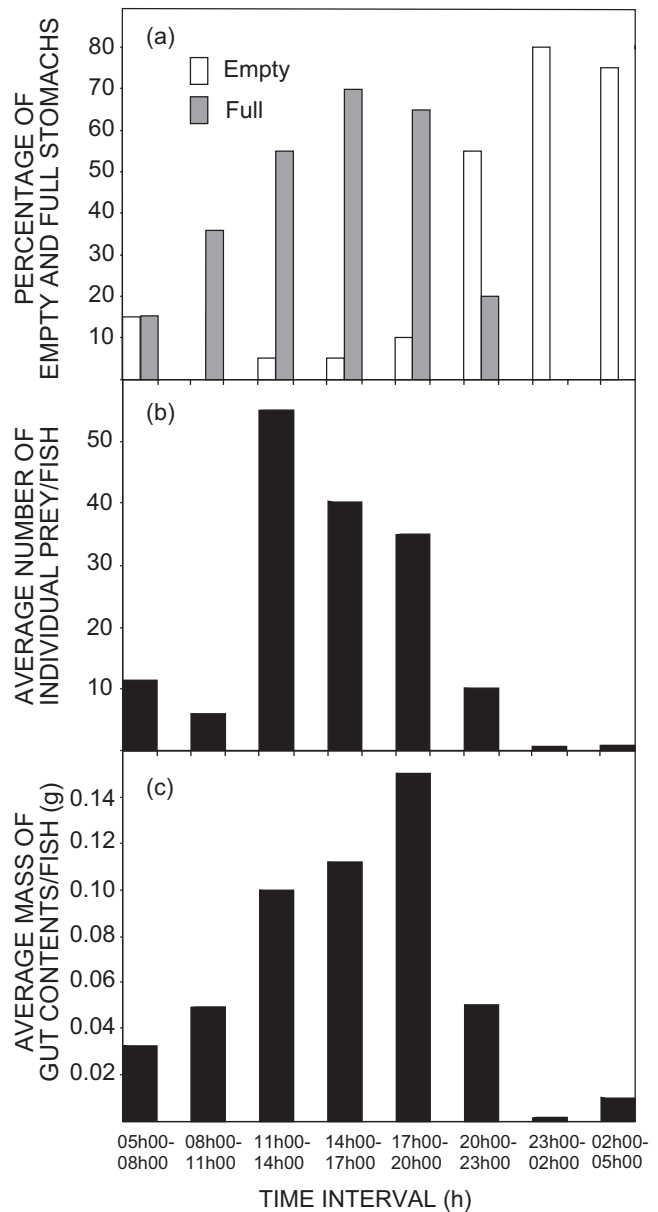
In contrast to *B. sadleri*, the catch of Nile perch was higher during the night in both exposed and wetland habitats (Figure 1). However, the difference between night and day catches was less pronounced than in *B. sadleri*. In the exposed area where Nile perch were most abundant, there was a clear peak in CPUE between 17h00 and 20h00; there was no strong peak in the wetland habitat, where Nile perch were far less abundant.

**Table 2:** Relative importance indices (RI) for prey items in the stomachs of *Brycinus sadleri* from the exposed site of Lake Nabugabo, Uganda, in 1995. Ephem. larvae = Ephemeroptera larvae, Ephem. adults = Ephemeroptera adults. A blank indicates a zero value

Number examined	RI — Exposed Site (1995)							
	20	20	20	20	20	20	10	10
Number with food	15	20	19	19	18	11	6	4
	05h00–08h00	08h00–11h00	11h00–14h00	14h00–17h00	17h00–20h00	20h00–23h00	23h00–02h00	02h00–05h00
Ephemeroptera:								
<i>Povilla</i> nymphs	11.39	50.29	36.00	38.32	53.87	41.58	36.41	37.95
Ephem. larvae (free swimming)	1.62		1.14	5.84		16.43		
Ephem. adults	22.53	1.76	4.49			9.84	26.88	20.86
Chaoboridae:								
Chaoborid larvae	11.60	4.04	29.32	10.03	38.51	2.88	10.29	14.39
Chaoborid pupae	23.12	4.74	4.81	38.30				
Chaoborid adults	9.64	1.57	1.16					
Chironomidae:								
Chironomid larvae								
Chironomid pupae		13.62	2.36	1.25	3.36	19.39		
Chironomid adults	14.65	8.30	5.45	1.25	2.35	4.07		20.86
Other prey:								
Ceratopogonid larvae		6.38	7.80		1.91			
Trichoptera larvae								
Trichoptera adults		1.76						
Hymenoptera			1.34	1.26		3.03		
Coleoptera								
Odonata nymphs			1.37					
Corixidae	3.18	5.63	2.39	2.50		2.78	26.42	
Ostracoda								
Hirudinea	2.25	1.91	2.37					
Invertebrate remains				1.24				5.94
Plant remains								

The numbers of individuals of different prey categories in the stomachs of *B. sadleri* were not independent of the time of day for both the exposed ( $\chi^2 = 7\ 143.2$ ,  $P < 0.001$ ) and wetland habitats ( $\chi^2 = 13\ 618.2$ ,  $P < 0.001$ ). Because *B. sadleri* were most abundant in the exposed habitat, we focus on the results for stomach contents of specimens collected from the exposed site and refer to a smaller sample of fishes collected from the wetland habitat. In the exposed habitat, *B. sadleri* began feeding between 05h00 and 08h00 (Figure 2). At this time, chaoborid pupae dominated the gut contents; other major prey items consisted of surface forms, such as Ephemeroptera adults, and chironomid adults (sub-families: Chironominae and Tanypodinae, Tables 2, 3 and 4). These seem to have been taken from the littoral areas where chironomids were most common. *Povilla adusta* nymphs and chironomid pupae and adults (mainly of the deep-water genus: *Procladius*) dominated the contents between 08h00 and 11h00. Feeding intensified between 11h00 and 14h00 as indicated by a sharp increase in the average number of prey items and prey biomass per fish (Figure 2, Tables 2 and 3). At this time, benthic prey (primarily chaoborid larvae and *Povilla adusta* nymphs) dominated the diet (Tables 2, 3 and 4) indicating that feeding was occurring at the bottom. However, there was an increase in the number of chironomid adults (mainly of the genus *Procladius*) in the stomachs suggesting some surface or water column feeding as well. Chaoborid pupae and *Povilla adusta* nymphs dominated the stomach contents from 14h00 until about 17h00. At this time, there was a decrease in the proportion of chaoborid larvae. Between 17h00 and 20h00, chaoborid larvae again became the most numerically abundant prey (Tables 2, 3 and 4). Between 20h00 and 23h00, littoral insects (*Povilla adusta* nymphs, Ephemeroptera free-swimming larvae, and chironomid pupae) once again became important in the stomachs; however, there was a marked decrease in feeding activity at this time as indicated by a sharp increase in the percentage of empty stomachs and a decrease in both the numbers and mass of prey (Figure 2). *Povilla adusta* nymphs always dominated the gut contents, mainly on account of their bulk rather than their numbers (Tables 2 and 3). Between 23h00 and 02h00 the stomachs of most fish were empty, but a few still had relict food. Results from the analysis of mass of gut contents followed those of numbers and RI very closely. The average mass of gut contents per fish increased steadily from dawn until the early evening and then decreased to very low levels by 23h00 (Figure 2, Table 3).

In the wetland habitat, the feeding pattern was very similar to that in exposed habitat. Between 05h00 and 08h00 *B. sadleri* fed mainly on the sub-imago or adults of Ephemeroptera, *Povilla adusta* nymphs, and chaoborid larvae and pupae. Between 08h00 and 11h00, the same types of prey dominated the stomach contents of *B. sadleri* as in the previous period; however, the proportion of Ephemeroptera adults decreased sharply. Between 11h00 and 14h00, the proportion of chaoborid pupae decreased; however, that of chaoborid larvae increased sharply, suggesting bottom feeding. Between 14h00 and 17h00, there was a decrease in the number and mass of chaoborid larvae and an increase in the number and mass of *Povilla adusta*



**Figure 2:** Feeding activity of *Brycinus sadleri* in an exposed site of Lake Nabugabo, Uganda in 1995. The bars represent a) the percentage of fish examined that had empty or full stomachs (expressed as a percentage of all stomachs examined), b) the average number of individual prey items per fish, and c) the average mass of gut contents per fish. Averages for b and c are based on the total number of fish examined for each time interval. Only stomachs rated as completely full or empty were used in the comparison of full and empty stomachs

nymphs and chaoborid adults. However, chaoborid larvae still dominated the gut contents. Some Hymenoptera and Isoptera were also represented, suggesting some surface and column feeding at this time. Between 17h00 and 20h00, chaoborid larvae and pupae, and chironomid pupae were the dominant prey.

**Table 3:** Total numbers of prey items recovered from the stomachs of *Brycinus sadleri* from the exposed site of Lake Nabugabo, Uganda, in 1995. Average number of prey items per fish is calculated as the total number of prey items in the stomachs for a time interval divided by the total number of fish examined for that time interval. Ephem. larvae = Ephemeroptera larvae, Ephem. adults = Ephemeroptera adults. A blank indicates zero values

Number examined	Numbers of prey items — Exposed Site (1995)							
	20	20	20	20	20	20	20	10
Number with food	15	20	19	19	18	11	6	4
	05h00–08h00	08h00–11h00	11h00–14h00	14h00–17h00	17h00–20h00	20h00–23h00	23h00–02h00	02h00–05h00
<b>Ephemeroptera:</b>								
<i>Povilla</i> nymphs	4	55	58	37	31	32	2	2
Ephem. larvae (free swimming)	1		1	24		68		
Ephem. adults	38	1	17			6	2	1
<b>Chaoboridae:</b>								
Chaoborid larvae	39	6	933	35	671	2	1	1
Chaoborid pupae	75	3	12	683				
Chaoborid adults	18	1	2					
<b>Chironomidae:</b>								
Chironomid larvae								
Chironomid pupae		25	6	1	2	64		
Chironomid adults	31	17	44	1	10	7		1
<b>Other prey:</b>								
Ceratopogonid larvae		4	27		4			
Trichoptera larvae								
Trichoptera adults		1						
Hymenoptera			3	1		1		
Coleoptera								
Odonata nymphs			1					
Corixidae	2	6	4	2		1	3	
Ostracoda								
Hirudinea	1	1	2					
Invertebrate remains								
Plant remains								
Total no. of prey items	209	120	1110	784	718	181	8	5
Average no. of prey items fish	10.45	6.00	55.50	39.20	35.90	9.05	0.40	0.50

The strong shifts in the diet of *B. sadleri* over the day to include different taxa from different habitats (surface vs bottom) were reflected in relatively low overlap in diet between any two time periods. We used the Morisita's index of similarity to compare the overlap in gut contents between time periods for the exposed habitat where stomach contents were analysed for each period of the 24h cycle. Similarity was low, averaging 66% and ranging between 39% and 91% (Table 5).

The feeding activity of Nile perch was evaluated through analysis of stomach contents from a 24h beach seine sample that produced 412 stomachs. The proportion of full stomachs was not independent of the time of day ( $\chi^2 = 3\,905.08$ ,  $P < 0.001$ ) and was lowest between 12h00 and 14h00 (Figure 3). The proportion of full stomachs increased rapidly to a peak between 18h00 and 20h00 and was high throughout the night. The proportion of full stomachs was low by early morning and remained so throughout the day; however, the presence of some full stomachs during each daylight sampling period suggests that Nile perch do continue to feed at a low level during the daylight hours. The stomach con-

tents of Nile perch collected from the beach seine, as well as the diel samples and habitat wide survey in 1995 (total number of non-empty stomachs = 364) are detailed in Schofield (1997) and Schofield and Chapman (1999).

To summarise, Nile perch showed a strong shift from invertebrate feeding to piscivory at approximately 30cm (total length). Major fish prey included *R. argentea* and juvenile Nile perch. Other species, including *B. sadleri* of which only three specimens were recovered from Nile perch stomachs, were rare in their diet.

## Discussion

*Brycinus sadleri* has shown remarkable persistence in lakes into which Nile perch have been introduced. Our results suggest that their diel pattern of behaviour and habitat use may have helped to minimise interactions with foraging Nile perch.

Both Nile perch and *B. sadleri* were more abundant in the offshore areas of exposed transects than in wetland areas. This may relate in part to the lower levels of dissolved



**Table 4:** Total mass of prey recovered from the stomachs of *Brycinus sadleri* from the exposed site of Lake Nabugabo, Uganda, in 1995. Average mass of gut contents per fish is calculated as the total mass of gut contents for a time interval divided by the total number of fish examined for that time interval. Ephem. larvae = Ephemeroptera larvae, Ephem. adults = Ephemeroptera adults. A blank indicates zero values

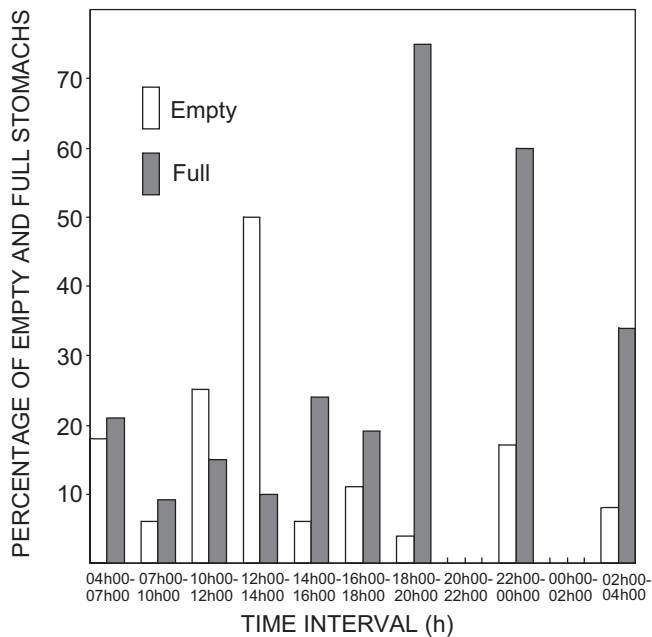
Number examined	Mass of prey items — Exposed Site (1995)							
	20	20	20	20	20	20	20	10
Number with food	15	20	19	19	18	11	6	4
	05h00–08h00	08h00–11h00	11h00–14h00	14h00–17h00	17h00–20h00	20h00–23h00	23h00–02h00	02h00–05h00
Ephemeroptera:								
<i>Povilla</i> nymphs	0.15	0.86	1.44	1.53	2.60	0.85	0.03	0.02
Ephem. larvae (free swimming)				0.14		0.04		
Ephem. adults	0.24	0.01	0.08			0.06	0.02	0.01
Chaoboridae:								
Chaoborid larvae	0.05		0.18	0.04	0.27			
Chaoborid pupae	0.07		0.02	0.44				
Chaoborid adults	0.02							
Chironomidae:								
Chironomid larvae								
Chironomid pupae		0.12	0.01			0.09		
Chironomid adults	0.08	0.03	0.13		0.03	0.02		0.01
Other prey:								
Ceratopogonid larvae		0.01	0.07		0.01			
Trichoptera larvae								
Trichoptera adults		0.01						
Hymenoptera			0.02			0.02		
Coleoptera								
Odonata nymphs			0.02					
Corixidae		0.01	0.01			0.01	0.01	
Ostracoda								
Hirudinea	0.02	0.01	0.01					
Invertebrate remains								0.01
Plant remains								
Total mass of gut contents	0.62	1.05	1.99	2.15	2.91	1.08	0.06	0.06
Average mass of gut contents per fish	0.03	0.05	0.10	0.11	0.15	0.05	0.00	0.01

**Table 5:** Morisita's indices comparing overlap in gut contents among *Brycinus sadleri* captured at different times of day in the exposed site of Lake Nabugabo, Uganda, in 1995. Values over 0.85 are in bold. The time represents the beginning of the sampling interval

	08h00	11h00	14h00	17h00	20h00	23h00	02h00
05h00	0.43	0.59	0.75	0.39	0.46	0.60	0.60
08h00	0.76	0.75	0.78	<b>0.88</b>	0.69	0.54	
11h00		0.74	<b>0.91</b>	0.72	0.68	0.80	
14h00			0.69	0.69	0.56	0.49	
17h00				0.71	0.65	0.77	
20h00					0.72	0.53	
23h00						0.60	

oxygen that characterise the wetlands, particularly the ecotonal areas. Nile perch are relatively intolerant of hypoxia (Schofield and Chapman 2000, Chapman *et al.* 2002) and are rarely encountered in hypoxic waters. Our anecdotal observations and haematological data (Chapman *et al.* 2002) suggest that *B. sadleri* may also be relatively sensitive to hypoxia stress, though it may encounter periodic hypoxia

during benthic feeding. Despite similar broad distributional patterns within Lake Nabugabo, the overlap in habitat use between *B. sadleri* and Nile perch may not result in a high level of interaction if their activity patterns differ. We found evidence for a strong diel shift in activity and modest changes in the habitat use of *B. sadleri* that may permit persistence with Nile perch. In general, *B. sadleri* was active



**Figure 3:** The percentage of Nile perch (*Lates niloticus*) in the exposed site of Lake Nabugabo, Uganda (1995) with empty and full stomachs (expressed as a percentage of all stomachs examined). Each point or bar represents the average of two sampling periods. Only stomachs rated as completely full or empty were used in the comparison of full and empty stomachs

and actively foraging during the daylight hours, while Nile perch began actively foraging during the early evening and was more active during the night than during the day. However, the early evening was characterised by a relatively high level of feeding activity in both species.

*Brycinus sadleri* began foraging in the early morning. Prior to this period they had little or no food in their stomachs, thus their heightened activity following sunrise seemed to be due to foraging. At this time they fed primarily on emerging adult and sub-adult insects (Ephemeroptera, chironomids and chaoborids) at the surface or in the water column. The increase in their numbers 100m offshore in the early morning suggests some offshore movement at this time. Then, as light levels increased, they showed a shift to benthic feeding. Offshore feeding during the day was evident in the characteristics of their benthic prey base and the low relative abundance of fish in the inshore net between 11h00 and 14h00. There was a large increase in larval and pupal forms of dipteran insects (particularly chaoborid larvae) and *Povilla adusta* in the stomachs of *B. sadleri* during the day. Our 20m offshore and 100m offshore nets were set at sites that averaged 2m and 3m in depth, respectively. In exposed areas of Lake Nabugabo Olowo (1998) found chaoborid larvae and *Povilla adusta* to be most abundant in the 3–4m depth zone and the 2–3m depth zone respectively. In their study of benthic invertebrates in Lake Nabugabo, Efitre *et al.* (2001) reported the highest densities of chaoborid larvae in the 2–3m depth zone. *Povilla adusta* were most common in wetland ecotones, but in open waters

showed a peak in the 2–3m depth zone (Efitre *et al.* 2001). Ceratopogonid larvae also appeared in the stomachs of fish in the midday period. Like chaoborid larvae, the ceratopogonid larvae occur mostly in deep waters (Merritt and Cummins 1984) and were most abundant in the 3m depth zone in Lake Nabugabo (Olowo 1998). By the late afternoon, most fish had full stomachs dominated by benthic prey. Benthic feeding may have contributed to a decrease in CPUE in the exposed habitat during the mid-day period. Fish may be less active during benthic feeding than when feeding in the water column and less easily captured at the furthest offshore site where the depth of the water precluded full coverage of the water column by the floating net. There was some evidence to suggest movement of *B. sadleri* back to shore later in the day as indicated by the large increase in the CPUE in the littoral areas, particularly the 5m net zone, between 17h00 and 20h00. They generally remained quiet for the rest of the night. By 23h00, most fish had empty stomachs and, during the night, most were captured in the net closest to shore. The evening crepuscular period was characterised by a high level of foraging activity in Nile perch, and access to inshore structure may be particularly important at this time. This diel activity and foraging pattern of *B. sadleri*, involving changes in its distribution and activity, may minimise its interactions with Nile perch. *Brycinus sadleri* feeds primarily when the predator is less active and decreases its activity or shifts its distribution when the predator becomes active.

Many extant haplochromines and several non-cichlids have persisted with Nile perch by using various structural and/or low oxygen refugia (Chapman *et al.* 1996a, 1996b, Seehausen 1996, Rosenberger and Chapman 1999, 2000, Schofield and Chapman 1999, 2000). *Brycinus sadleri* appears to use behavioural mechanisms to avoid predators through a diel pattern of activity and distribution that permits overlap in habitat use but minimises exposure to foraging Nile perch. There is no evidence that it uses low-oxygen refugia, as it has never been reported from habitats characterised by extreme hypoxia in Lake Nabugabo (Chapman 1996b, Rosenberger and Chapman 1999). However, access to inshore structure may be important, particularly during the evening when Nile perch feeding seems to be most intense.

Both Nile perch and *B. sadleri* appear to be visual predators. However, Nile perch seems to forage most effectively under low light, whereas *B. sadleri* forages primarily in daylight hours. *Brycinus sadleri* seems to shift from surface to benthic feeding as light levels increase, which may decrease their susceptibility to visual predators during the daylight hours. It is curious that *B. sadleri* does not exploit chaoborid larvae and pupae at night, when these are most active in the water column (Merritt and Cummins 1984) and potentially easier to capture. This may reflect a response to the nocturnal foraging activities of Nile perch; although comparative diel data from lakes without Nile perch will be necessary to confirm the presence of a behavioural shift in the activity pattern of *B. sadleri* in lakes with Nile perch.

Although *B. sadleri* has shown great resilience to the introduction of Nile perch, Chapman *et al.* (2003) noted a decline in this species in Lake Nabugabo between 1995 and 2000, which coincided with a resurgence of other indigenous

fishes, in particular haplochromine cichlids, in that lake. In 1995 haplochromine cichlids were largely confined to inshore areas, particularly wetland ecotones, and were rare in Nile perch stomachs, as were most other indigenous species. By 2000 haplochromine cichlids were abundant in inshore and offshore areas of both exposed and wetland transects. Several indigenous non-cichlids also reappeared in the main lake, including three of the four original mormyrid species (Chapman *et al.* 2003). Over this time, the mean CPUE (number per transect) of *B. sadleri* declined dramatically from 92 fish per transect in 1995 to 16 fish per transect in 2000. It is possible that the resurgence of insectivorous haplochromines in Lake Nabugabo has increased competition for this food base and contributed to the decline of *B. sadleri*. A much longer time series of data on the fish community structure in Lake Nabugabo will be necessary to confirm the dynamics of the native and introduced species in this system and the impact of faunal collapse and recovery on the *B. sadleri* population.

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