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OBSERVATIONS ON SYNCHRONOUS AIR BREATHING IN *CLARIAS LIOCEPHALUS*.—

Several accounts of air-breathing fishes from a variety of phylogenetic lineages include observations of synchronous air breathing, whereby individuals in a group breathe together or in rapid succession (e.g., *Lepisosteus osseus*, *Lepisosteus oculatus* Hill, 1972; *Hoplosternum thoracatum*, *Piabucina festae*, *Trichogaster leeri*, *Ancistrus chagresi*, Kramer and Graham, 1976; *Hypostomus plecostomus* Graham and Baird, 1982). It has been suggested that the selective factor underlying synchrony is predation pressure, with clumped breaths functioning to reduce the potential for contact between predator and prey in an analogous manner to schooling (Kramer and Graham, 1976; Gee, 1980; Baird, 1983). Synchronous air breathing is all the more remarkable when one considers that individuals differing in activity or size are likely to have different respiratory requirements.

We report observations on the air-breathing behavior of *Clarias liocephalus* in semicontrolled conditions near a papyrus swamp in western Uganda. A previous study has demonstrated that the air-breathing behavior of *Clarias batrachus* is often synchronous (Loftus, 1979). We look for evidence of synchronous air breathing in a second species of *Clarias* and examine the behavior of individuals during breathing bouts.

The study was conducted in the Kibale Forest Reserve, Uganda, and is part of a larger study on the ecology of fishes in papyrus swamps. *Clarias liocephalus* is a small clariid catfish (maximum total length = 27 cm in the Kibale Forest) that is widely distributed in East Africa (Teugels, 1986). In the Kibale Forest Reserve, *C.*

liocephalus is found in most aquatic habitats including small intermittent streams, forest marsh pools, papyrus swamps, and everflowing rivers. Aerial respiration in *Clarias* involves the periodic intake of air into highly vascularized suprabranchial chambers (Donnelly, 1973; Liem, 1987). Like many members of the genus, *C. liocephalus* is also capable of invading terrestrial habitats for short periods. Study specimens were captured from a papyrus swamp, held in a small (1.5 m diameter) pond, and fed on fresh fish and insects. Eight fish (mean total length = 15.9 cm) were individually marked by injecting tattoo ink subdermally with a fine gauge hypodermic needle (Thresher and Gronell, 1978). Fish were paired by size, and pairs were divided to produce two groups of approximately equal size variation (total lengths of group 1: 23.5 cm, 15.8 cm, 12.3 cm, and 9.5 cm; group 2: 26.4 cm, 15.8 cm, 13.6 cm, and 10.3 cm). The groups were transferred to separate buckets (water depth = 16 cm, bucket diameter = 47 cm, bucket height = 23 cm) 2 h prior to the initiation of observations. Dissolved oxygen concentration was lowered to approximately 0–0.1 mg/liter by the addition of small amounts of sodium sulfite. Water temperature averaged 18.1 C and ranged from 17.0–19.4 C.

Each group of four fish was observed for 30 min with the occurrence of each breath and the identity of the breather recorded to the nearest sec. After observing the group, three fish were removed from each bucket and transferred back to the pond, leaving the largest or smallest fish in the bucket. After 1 h, air breaths of the solitary fish were recorded. Six replicate observations were conducted on each group and the solitary fish, with groups alternated between buckets, and removal of the three largest or three smallest assigned randomly to the buckets on a daily basis.

Following Kramer and Graham (1976), Loftus (1979), and Baird (1983), we looked for synchrony by quantifying the temporal frequency distribution of the breaths. Observation periods were divided into 100-sec intervals for solitary fish and 25-sec intervals for groups of four fish, because the total number of breaths was far less for solitary fish. The frequency distribution of the number of breaths per interval was analyzed for clumping by calculating the Coefficient of Dispersion (CD, variance/mean ratio, Sokal and Rohlf, 1981). CD is a descriptive statistic that will be greater than 1.0 for clumped distributions and less than 1.0 for uniform distributions. The significance of the difference between the observed coefficient and unity was determined by comparing the difference with its standard

TABLE 1. THE MEAN RATES OF BREATHING PER SAMPLE INTERVAL (B/I) AND THE RATIO OF THE VARIANCE TO THE MEAN FOR THE BREATHS PER INTERVAL (COEFFICIENT OF DISPERSION, CD) FOR *Clarias liocephalus* IN GROUPS OF FOUR FISH AND AS SOLITARY FISH. All observation sets are 30-min intervals. The number of breaths that occurred within 5 sec of a previous breath was recorded and expressed as a percentage of the total breaths occurring during each observation period (5-sec synchrony).

Observation set	No. of intervals	Length of interval (sec)	B/I	CD	P value	5-sec synchrony
01—solitary	18	100	1.39	1.79	<0.05	
02—solitary	18	100	0.61	0.41	n.s.	
03—solitary	18	100	0.72	0.95	n.s.	
04—solitary	18	100	0.67	1.24	n.s.	
05—solitary	18	100	1.33	0.62	n.s.	
06—solitary	18	100	0.39	0.65	n.s.	
07—solitary	18	100	0.94	0.56	n.s.	
08—solitary	18	100	0.28	0.77	n.s.	
09—solitary	18	100	1.06	1.06	n.s.	
10—solitary	18	100	1.33	1.15	n.s.	
11—solitary	18	100	1.56	0.70	n.s.	
12—solitary	18	100	0.56	1.10	n.s.	
01—group	72	25	0.96	1.69	<0.001	45.5
02—group	72	25	1.35	0.94	n.s.	32.0
03—group	72	25	0.38	1.46	<0.005	55.6
04—group	72	25	0.63	1.28	n.s. (<0.10)	37.8
05—group	72	25	0.38	2.21	<0.001	74.1
06—group	72	25	1.36	1.35	<0.05	46.9
07—group	72	25	0.51	1.81	<0.001	73.0
08—group	72	25	0.57	1.53	<0.005	48.8
09—group	72	25	0.78	1.60	<0.001	46.4
10—group	72	25	0.94	1.70	<0.001	50.0
11—group	72	25	0.90	1.50	<0.005	71.0
12—group	72	25	0.93	1.04	n.s.	27.7

error using a t-test (Grieg-Smith, 1964; Kramer and Graham, 1976; Baird, 1983).

For solitary individuals, the CD averaged 0.92 (range = 0.41–1.79). Only one sample showed a clumped distribution of air breaths. In the remaining 11 samples, the distribution of breaths did not differ significantly from random (Table 1).

There was no significant difference between the two groups of four fish in the average number of breaths per interval (t-test, $t = 1.22$, $P = 0.25$) or in the average CD (t-test, $t = 0.97$, $P = 0.36$). Breathes were clumped ($P < 0.05$, two-tailed test) in nine out of 12 of the observation periods for *C. liocephalus* groups (mean CD = 1.51, range = 0.94–2.21, Table 1). Although the air-breathing trips of grouped *C. liocephalus* were clumped in most samples, trips to the surface were generally not simultaneous but occurred in rapid succession (within 5 sec). It was rare for all individuals in the group to participate in the same trip to the surface, and isolated breaths occurred on a number of occasions. Thus, even a sampling interval of 25 sec could

encompass a tightly synchronized group of breaths and individual breaths spaced 10–15 sec apart. In the CD analysis of 25-sec intervals, we did not differentiate between successive breaths by the same fish and successive breaths by two or three different fish. To examine synchrony on a finer temporal scale, we calculated the number of breaths that occurred within 5 sec of a previous breath by a different fish and expressed these breaths as a percentage of the total breaths recorded during each observation period (Baird, 1983). On average, 50.7% of the breaths occurred within 5 sec of a prior breath by a different fish (range = 27.7–74.1%, Table 1). The percent frequency of 5-sec synchrony was correlated with the CD ($r = 0.83$, $P = 0.002$), supporting our interpretation of synchrony in the breathing behavior of groups of *C. liocephalus*. Only two fish participated in 75% of the bouts where breaths were no more than 5 sec apart. In 19% of the bouts, three fish participated, whereas all four fish participated in 6% of the total breathing bouts.

To examine the influence of body size on the

participation of individuals in synchronous bouts, we first compared the incidence of 5-sec synchrony in fish ranked 1–4 by size. There was no difference among size classes in the proportion of breaths that occurred in 5-sec synchrony ($\chi^2 = 2.4$, $df = 3$, $P > 0.10$). In addition, for synchronous breathing bouts with only two participants, fish were no more likely to breathe with a fish of an adjacent size class than with a fish much larger or smaller ($\chi^2 = 0.26$, $df = 1$, $P > 0.50$). Further, there was no difference between the largest and smallest fish in either the mean number of breaths per sample (paired t-test, $t = 0.66$, $P = 0.523$) or in the proportion of synchronous bouts (<5 sec apart) initiated by the largest and smallest fish ($\chi^2 = 0.025$, $df = 1$, $P > 0.50$).

Fish showed intention movements prior to air breathing which may have provided a cue to the other fish. The fish that initiated a trip to the surface would often start by swimming slowly along the bottom in an agitated fashion. This behavior appeared contagious, initiating agitated movements among other members of the group. In contrast to the slow movement before air breaths, trips to the surface were extremely rapid. Individual *C. liocephalus* were generally in close proximity to one another, and fish participating in a breathing bout would often surface near the same area in rapid succession. Occasional observations of *C. liocephalus* during the night in holding ponds have shown much more uniform spacing of individuals, and nighttime breathing patterns may differ from those observed during the day.

Modes of ventilation in clariid catfishes have been studied in some detail. *Clarias lazera*, *C. batrachus*, and *C. gariepinus* exhibit two modes: triphasic ventilation, whereby exhalent gas is expelled by creating a draft of fresh air which passes from the buccal cavity into the air chamber, replacing the stale air which escapes through the opercular openings, and quadruphasic ventilation, whereby water is used to expel the exhalent gas from the air chamber before inhalation (Donnelly, 1973; Hellin and Chardon, 1983; Liem, 1987). The triphasic mode is only used in very shallow water (less than a few cm) when water levels are inadequate for quadruphasic breathing or when the fish is out of the water (Liem, 1987). Our observations of the breathing cycles of *C. liocephalus* concur with these previous studies of other *Clarias* species. We used a video recording of a group of *C. liocephalus* in a small aquarium to examine the breathing cycle in more detail. During trips to the surface, bubbles were generally released prior to breaking the surface and reached the sur-

face as the fish was turning to return to the bottom. Quadruphasic ventilation may minimize surface exposure, because the bubbles tend to reach the surface as the fish is retreating. In addition, quadruphasic breathing generally demands less time at the surface than triphasic breathing.

Previous reports of increased synchrony in response to disturbance support its evolution as a predatory defense (Gee, 1980; Baird, 1983). In our examination of air breathing in *C. liocephalus*, the maintenance of synchrony by groups of individuals varying in size and breathing rates supports strong selection for synchronous breathing. Rapid trips to the surface, spatial and temporal synchrony in air-breathing trips, and the pattern of exhalation in *Clarias liocephalus* may minimize the risk associated with trips to the surface.

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