

Aerial and aquatic feeding in the silver arawana, *Osteoglossum bicirrhosum*

Dayv Lowry^a, Alpa P. Wintzer^{a,b}, Michael P. Matott^{a,c}, Lisa B. Whitenack^a, Daniel R. Huber^a, Mason Dean & Philip J. Motta^a

^aDepartment of Biology, University of South Florida, SCA 110, 4202 East Fowler Avenue, Tampa, FL 33620-5200, U.S.A

^bU.S. Fish and Wildlife Service, 4001 North Wilson Way, Stockton, CA 95205, U.S.A

^cEckerd College, Natural Sciences Collegium, 4200 54th Avenue South, St. Petersburg, FL 33711, U.S.A.

^dEcology and Evolutionary Biology, University of California Irvine, 321 Steinhaus Hall, Irvine, CA 92697, U.S.A

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Synopsis

The silver arawana, *Osteoglossum bicirrhosum*, hunts along shorelines and within flooded forests in the Amazon River basin and supplements its limited consumption of aquatic vertebrates by leaping from the water to obtain terrestrial and arboreal prey. We offered *O. bicirrhosum* prey both suspended above and submerged below the surface of the water. From high-speed digital recordings, we measured kinematic variables associated with the jaws, cranium, pectoral fins, and body during orientation and prey capture. Aquatic and aerial feeding events were kinematically distinct, with aerial events generally involving faster, larger movements and a distinct delay in the onset of lower jaw depression until the head had left the water. The comparatively large gape during leaping may facilitate prey capture by overcoming variability in the apparent position of the prey due to refraction, while the delayed onset of mouth opening may serve to reduce the effects of drag. This distinctive leaping behaviour allows exploitation of the terrestrial prey base, especially during seasonal inundation of the Amazon River basin when the aquatic food base is widely dispersed.

Introduction

Studies of prey capture in lower vertebrates typically focus on organisms that feed exclusively in either aquatic or terrestrial environments throughout their lives. Many organisms, however, exploit prey in both aquatic and terrestrial environments. Such versatility in feeding behaviour can exist concomitantly with discrete metamorphic stages (Gans & Gorniak 1982, Nishikawa & Cannatella 1991, Reilly 1996), or within a single life-history stage (Summers et al. 1998, Deban & Marks 2002, Luiselli et al. 2002). Few kinematic and behavioural studies have focused specifically

on fishes that feed in both aquatic and aerial environments during the same life history stage (Hyatt 1971, Zahl et al. 1977, Seghers 1978, Sponder & Lauder 1981). The employment of a feeding repertoire that exploits disparate prey bases can expand an organism's ecological niche, potentially granting a competitive advantage in nutrient acquisition capacity.

Exploitation of non-aquatic food items by fishes has been documented in species that knock prey items into the water and subsequently consume them, as well as in species that obtain food while out of the water. The archer fish, *Toxotes chatareus*, obtains prey by projecting a stream

of water from its mouth to dislodge insects from low-hanging branches, in addition to capturing prey by leaping (Verwey 1928, Rossel et al. 2002, Timmermans & Souren 2004). The African tetras, *Brycinus nurse* and *Alestes baremoze*, leap up to 1 m into the air to dislodge seeds from the panicles of rice plants and consume them after they have fallen into the water (Matthes 1977). The Atlantic mudskipper, *Periophthalmus barbarus*, crawls from the water to feed on terrestrial arthropods (Sponder & Lauder 1981, Harrison & Miller 1992), while the four-eyed fish, *Anableps anableps*, Hart's Rivulus, *Rivulus hartii*, Atlantic salmon, *Salmo salar*, the sea trout, *Salmo trutta*, the freshwater butterflyfish, *Pantodon buchholzi*, and the silver arawana, *Osteoglossum bicirrhosum* are all reputed to leap from the water to capture prey aerially (Kalleberg 1958, Hyatt 1971, Zahl et al. 1977, Seghers 1978, Goulding 1980). Despite numerous studies describing behavioural aspects of feeding in both aerial and aquatic media, detailed studies comparing kinematics between the two media are largely lacking.

We chose the silver arawana *Osteoglossum bicirrhosum* (Cuvier 1829) as the subject of this study because accounts of its feeding behaviour, diet, and distribution are readily available, and because it is known to capture prey in both aquatic and aerial media. *Osteoglossum bicirrhosum* is a generalist predator in the Amazon River basin that inhabits shallow, blackwater lagoons and the littoral zone of rivers and lakes year-round, as well as invading the flooded forest during high water periods (Saint-Paul et al. 2000). It is a species of high commercial fisheries value (Lowe-McConnell 1975), despite comprising only a small percentage of the available fish biomass (Tejerina-Garro et al. 1998). Although *O. bicirrhosum* regularly feeds aquatically, it also leaps from the water to ambush prey on low-hanging branches (Lowe-McConnell 1964, Goulding 1980). Prey capture via leaping allows *O. bicirrhosum* to exploit an arboreal and terrestrial prey base comprised of insects, spiders, and a variety of small vertebrates during both the high and low water seasons (Goulding 1980). Fishes make up only a small portion of the diet of *O. bicirrhosum* regardless of season (Goulding 1980), further emphasizing the ecological importance of terrestrial prey to this species. The ballistic propulsion of *O. bicirrhosum* from the

water represents a method of capturing aerial prey for which cranial and body motions have never been thoroughly studied. Our goal was therefore to determine how the prey capture kinematics of *O. bicirrhosum* differ between aquatic and aerial feeding events and investigate the functional basis of these differences.

Materials and methods

Experimental protocol

We obtained four juvenile *Osteoglossum bicirrhosum* (10.1–17.6 cm Standard Length) through the aquarium trade and maintained them at the University of South Florida in two 435 l aquaria, split with dividers to accommodate two individuals each. A 12:12 L:D photoperiod was maintained throughout the study and water temperature ranged from 23 to 27°C. Standard length of the experimental animals increased by an average of 25% over the course of this study, a fact that we accounted for during statistical analysis by using regressions. For 1 month prior to data collection, we trained individuals to feed on house crickets, *Acheta domesticus* (Linnaeus 1758) that were rigidly held by forceps. We used attached prey to standardize the presentation treatment both above and below the water and to simulate aerial prey perched on overhanging foliage. During training sessions, the tank was illuminated by two 500-Watt quartz-halogen lights to condition the fish for filming sessions. We offered prey approximately one third of the fish's total length, above (aerial presentation treatment) or below (aquatic presentation treatment) the surface of the water.

We recorded feeding events digitally using two synchronized Redlake Motionscope high-speed cameras (Redlake, San Diego, CA, USA) recording at 500 frames per second. One camera recorded an orthogonal lateral view of the feeding event, while the other filmed a mirror placed at a 45° angle above the tank, providing an orthogonal dorsal view. Illumination was identical to that provided during training sessions, with a 20-min acclimation period prior to feeding. We denied individuals food for 24 h prior to filming to facilitate active feeding. Additionally, no more than the first seven feeding events per day were analyzed

to avoid the effects of satiation on kinematics (Sass & Motta 2002). Evidence of satiation was apparent as a decreased willingness to actively engage in feeding activity.

Video analysis

We analyzed five feeding events per individual in which the fish fed in a plane orthogonal to the lateral camera for both aquatic and aerial presentation treatments, yielding a total of 40 captures. We quantified timing variables relative to the time at which lower jaw depression began (time 0 ms), also termed the strike onset (Cook 1996). Note that in aerial feeding events, several behavioural actions occurred before the onset of lower jaw depression, generating negative values for the associated variables. We quantified kinematic variables related exclusively to cranial motion during the course of the capture sequence. These variables consisted of the following, with descriptions given for uncommon measurements: 1) time to maximum gape (ms); 2) maximum gape distance (cm); 3) maximum gape duration (ms); 4) time to onset hyoid depression (ms); 5) time to onset cranial elevation (ms); 6) time to maximum cranial elevation (ms); 7) maximum cranial elevation angle (degrees) = angle from the rostrum to the point where the cranium joins the body, to a line extending anteriorly along the dorsal surface of the body; 8) lower jaw elevation duration (ms); and 9) strike duration (ms) = from strike onset until jaw closure on prey. For aerial feeding events, the time that the rostrum broke the surface of the water (ms) was also noted as a reference point for determining which cranial motions occurred in the aquatic and aerial media.

We quantified several additional kinematic variables at or relative to attack onset, defined as the time at which the fish oriented to the prey and rapid forward motion of the body began (Cook 1996). The following variables were measured at attack onset, with descriptions given for uncommon measurements: 1) time to attack onset relative to strike onset (ms); 2) prey height/depth (cm); 3) body angle (degrees) = angle of the dorsal surface of the fish relative to the surface of the water; 4) relative total length contraction = the linear distance from the rostrum to the most posterior point on the tail when the fish is contracted into an

attacking posture, divided by the total length of the fish. By standardizing to total length we accounted for differences in apparent total length due to body angle; 5) pectoral fin sweep duration (ms) = from onset to cessation of motion of the pectoral fins; 6) pectoral fin sweep excursion (degrees); 7) pectoral fin sweep angular velocity (degrees $m\ s^{-1}$); 8) attack duration (ms) = from time of attack onset until jaw closure on prey; and 9) average attack velocity (SL s^{-1}) = calculated from the velocity of a fixed point on the head measured between alternating frames from attack onset to prey contact. We employed Redlake Motionscope 2.21 and Sigma Scan Pro 4 (SPSS Inc.) imaging software to measure kinematic variables.

Statistical analysis

We log- or arcsine-transformed all data and tested for both normality and equality of variance, using Kolmogorov–Smirnov and Levene Median tests, respectively. Body angle data failed the test for normality and could not be normalized by additional transformation. We therefore performed a non-parametric Spearman correlation analysis on all data to determine which variables were correlated with standard length and prey height or depth. Because we detected correlation with either standard length or prey height or depth for several variables (maximum gape duration, strike duration, and attack duration) and correlation with both for several additional variables (maximum gape distance and lower jaw elevation duration), we performed a multiple linear regression for all variables and obtained studentized residuals from the common trend lines (Reist 1985, Quinn & Keough 2002). We performed this procedure to minimize the effects of individual growth and because prey height/depth could not be precisely controlled over the course of this study. We used the residuals obtained from the regression procedure for the analyses detailed below. We utilized an experimental alpha-acceptance level of 0.05 for all statistical tests unless otherwise noted.

For the subset of kinematic variables with a balanced design (Table 2), we performed a principal components analysis (PCA) based on a correlation matrix. Only principal components with eigenvalues greater than 1.0 were included in

further analysis. Additionally, only variables with component loading scores above 0.6 were considered to load heavily on the respective axis. To identify significant differences between presentation treatments (fixed effect tested over the interaction mean square) as well as among individuals (random effect tested over the residual mean square) in multivariate space, we analyzed factor loading scores for PC axes I and II together using a two-way, mixed-model MANOVA. Differences in multivariate space due to both presentation treatment and individual were detected with the MANOVA; however the accompanying univariate tests indicated that only differences in presentation treatment attributable to PC axis I were significant. In order to isolate the contribution of PC axis I kinematic variables to differences between presentation treatments, we performed one-way ANOVAs on each variable. For the variable that failed normality (body angle) we used a conservative p -value of 0.01. This method is valid because ANOVA is robust to considerable deviations from the assumption of normality (Zar 1999). To graphically compare the relative timing and duration of kinematic variables that constitute an attack, we scaled these variables to attack duration. Variables were scaled to attack duration because it was the only variable included in the PCA that did not differ between presentation treatments.

The reorientation of the body during some leaping events made measurement of variables impossible, producing an unbalanced data set. In these cases (Table 1), we utilized a paired t -test based on individual means for each variable to

identify differences between presentation treatments. Because each individual was represented by a mean in this data set, the variability within and between individuals could not be assessed or separated from other variability. In order to avoid type II errors, Bonferroni corrections were not applied to any statistical analyses (Cabin & Mitchell 2000, Moran 2003). We performed Spearman correlation analyses, t -tests, linear regressions, and ANOVAs with Sigma Stat Version 2.03 (SPSS Inc.), and the PCA and MANOVA with SYSTAT Version 10 (SPSS Inc.).

Results

A feeding event typically began with the fish increasing its swimming speed to rapidly approach the prey. As the fish neared to within approximately one body length of the prey, its swimming speed decreased and its body was bent into either an 'S'- or 'C'-shaped posture for the attack (attack onset). In the 20 aquatic feeding events recorded, we observed 'S' and 'C' postures (Webb 1984) in 11 and 9 events, respectively. However, we observed 'S' postures in all 20 aerial feeding events. This difference is reflected in the greater relative total length contraction of aerial feeding events ($p = 0.047$). Additionally, the results of the paired t -tests indicated that aerial events were characterized by greater pectoral fin sweep angular velocity ($p = 0.015$), an earlier time of onset hyoid depression ($p = 0.021$), and an earlier onset of ($p = 0.025$) and shorter time to maximum ($p = 0.025$) cranial elevation (Table 1). The prey

Table 1. Paired t -test results for kinematic variables associated with aerial and aquatic feeding events in *Osteoglossum bicirrhosum*.

Variable	Mean \pm SE		T	p
	Aquatic	Aerial		
Relative total length contraction	17.5 \pm 2.5	28.8 \pm 2.6	3.276	0.047
Pectoral fin sweep duration (ms)	34.3 \pm 4.7	24.3 \pm 1.3	-0.857	0.454
Pectoral fin sweep excursion (degrees)	41.5 \pm 7.6	93.7 \pm 4.5	2.826	0.066
Pectoral fin sweep angular velocity (degrees $m s^{-1}$)	1.3 \pm 0.2	4.4 \pm 0.3	5.067	0.015
Time to onset hyoid depression (ms)	84.5 \pm 15.4	13.9 \pm 1.3	-4.475	0.021
Time to onset cranial elevation (ms)	74.5 \pm 18.9	10.0 \pm 0.5	-4.200	0.025
Time to maximum cranial elevation (ms)	95.2 \pm 18.6	19.7 \pm 1.1	-4.167	0.025
Maximum cranial elevation angle (degrees)	25.5 \pm 3.0	34.0 \pm 3.0	1.929	0.149

We performed these tests using variables that contained one or more missing values. Bold face shows significant results ($p < 0.05$) ($N = 4$; $df = 3$).

capture kinematics differed distinctly between aerial and aquatic feeding events, with aerial events typically involving faster movements and larger displacements (Figure 1 and Tables 1 and 2). Strike duration was approximately three times longer for aquatic than aerial feeding events, reflecting the rapid nature of jaw movements associated with aerial prey capture events (Figure 2 and Table 2). Although the frequency of occurrence was not quantified, we occasionally observed missed prey capture attempts during aerial attacks but never during aquatic attacks.

All variables except maximum gape duration and attack duration loaded heavily on principal component axis I, and attack duration loaded heavily on principal component axis II (Figure 1 and Table 3). The combined principal component axes scores clearly separated in multivariate space (MANOVA, Pillai Trace $F_{6,64} = 2.422$; $p = 0.036$). Aerial events were characterized by kinematic events with shorter durations, greater average attack velocity, and a larger gape size than aquatic events (Figure 2 and Table 2). A presentation treatment effect was indicated by the two-way ANOVAs in every variable except attack duration (Table 2). When variables describing

capture in both aerial and aquatic treatments were scaled to attack duration, it was clear that these differences involved distinct changes in behaviour and were not simply an effect of increasing the speed of the entire feeding event during aerial captures (Figure 2). Specifically, the lower jaw did not begin to depress until after both the initiation of pectoral fin motion (resulting in a negative time to attack onset) and after the fish left the water in aerial feeding events (Figure 2).

Discussion

Aerial feeding events consistently involved faster and larger excursions than aquatic feeding events, perhaps due to differences in the physical attributes of air and water (Shaffer & Lauder 1988). Decreases in viscosity and density experienced by *Osteoglossum bicirrhosum* after passing from water to air during leaping account for an approximately 3.5-fold decrease in drag (Vogel 1994), which may account for greater, more rapid excursion of cranial elements. Additionally, the delay in onset of lower jaw depression during aerial capture may reduce the effects of drag in two ways. First,

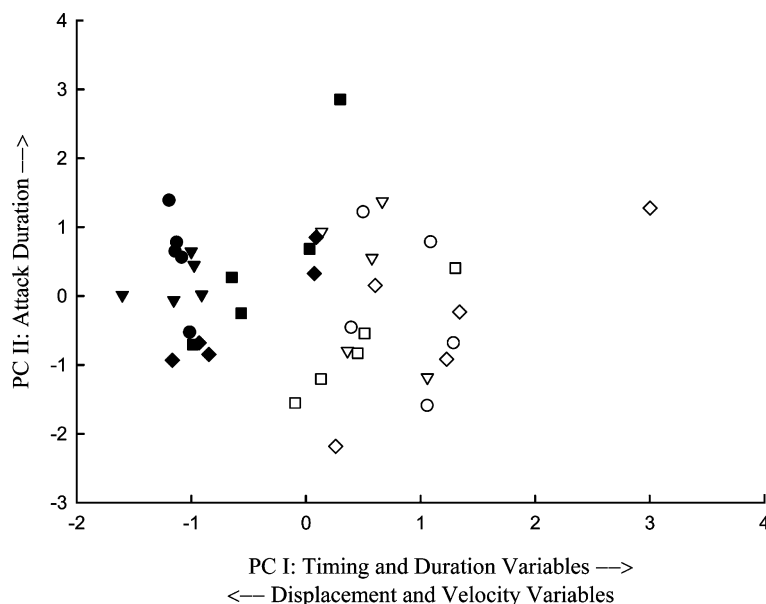


Figure 1. Principal components analysis of kinematic variables related to aquatic and aerial feeding events in *Osteoglossum bicirrhosum* showing factor loadings; solid shapes = aerial captures, empty shapes = aquatic captures, squares = fish 1, circles = fish 2, triangles = fish 3, diamonds = fish 4.

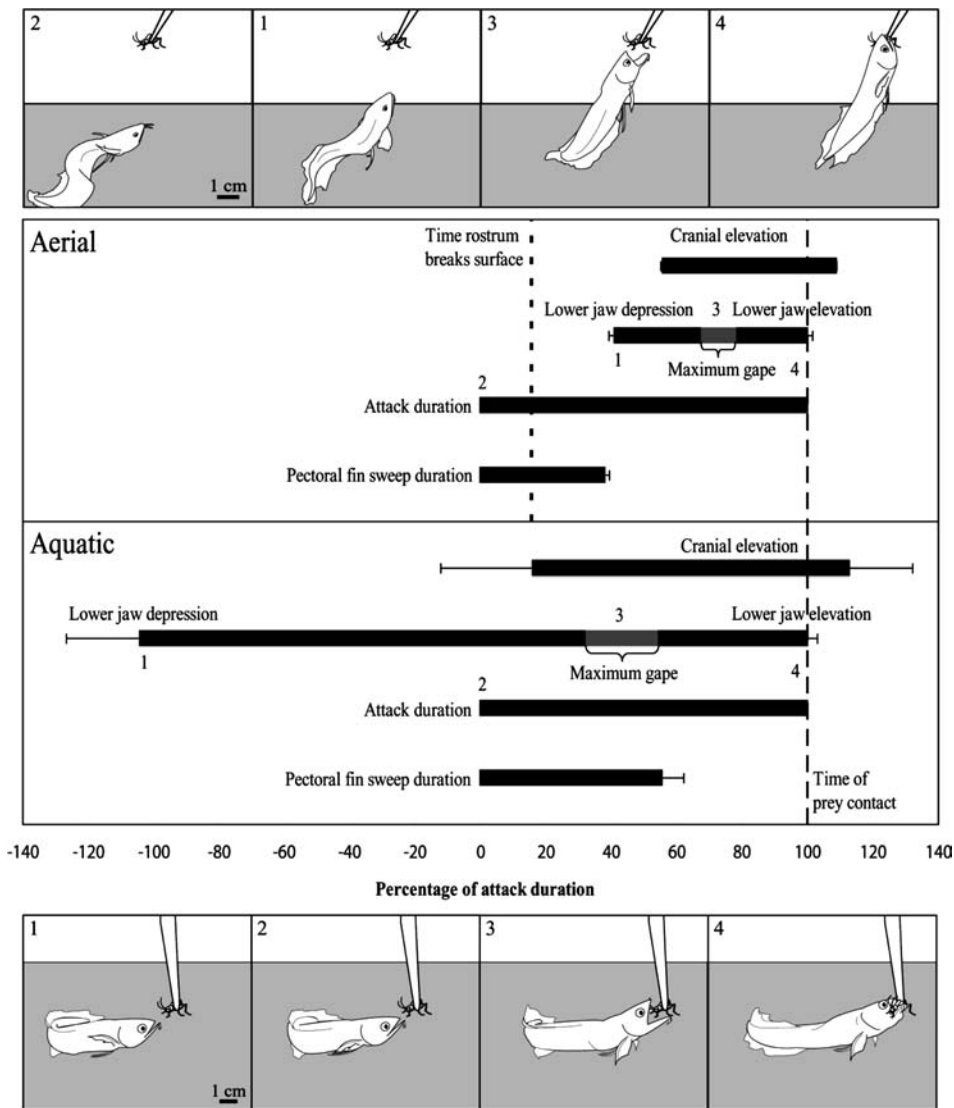


Figure 2. Comparison of aquatic and aerial feeding events in *Osteoglossum bicirrhosum*. Profiles of select kinematic variables describing aquatic and aerial feeding events are scaled as a percentage of attack duration. Values represent a mean for all sequences and error bars represent one standard error. Illustrations above and below the graph are taken from a representative aerial and aquatic feeding event, respectively. Numbers on these illustrations correspond to the respectively labeled portion of the graph and denote key kinematic events. 1 = onset lower jaw depression (strike onset); 2 = time of attack onset; 3 = time of maximum gape; 4 = time of prey contact. During aerial feeding events, the jaws open following attack initiation and after the rostrum of the fish breaks the surface of the water, while during aquatic feeding events the jaws open prior to attack initiation.

opening the mouth causes an increase in frontal area, or the cross-sectional area at the widest point of the fish perpendicular to the direction of motion (Vogel 1994), which reduces streamlining and increases drag. Second, if the mouth were opened prior to leaping, the buccal cavity would fill with water (Young 1991), requiring additional energy

expenditure to propel the fish and this added mass of water into the air. The delay of jaw opening to avoid these deleterious effects is functionally convergent with lateral head swiping as opposed to anteriorly-directed lunging during aquatic feeding in reptiles (Taylor 1987, Young 1991, Alfaro 2003).

Table 2. One-way ANOVA results for effects of presentation treatment (aquatic versus aerial) on kinematic variables associated with aerial and aquatic feeding events in *Osteoglossum bicirrhosum*.

Source of Variation	Mean \pm SE		MS	F	p
	Aquatic	Aerial			
Time to attack onset (ms)	62.5 \pm 14.9	-26.8 \pm 1.6	23.180	52.839	<0.001
Residual			0.439		
Body angle (degrees)	1.5 \pm 4.5	17.8 \pm 1.1	7.006	8.126	0.007
Residual			0.862		
Attack duration (ms)	63.0 \pm 4.1	66.1 \pm 4.0	0.488	0.467	0.498
Residual			1.046		
Average attack velocity (SL s ⁻¹)	3.0 \pm 0.4	9.2 \pm 0.5	22.127	48.397	<0.001
Residual			0.457		
Time to maximum gape (ms)	84.9 \pm 15.1	17.4 \pm 0.7	18.934	34.073	<0.001
Residual			0.556		
Maximum gape distance (cm)	1.8 \pm 0.1	3.0 \pm 0.2	22.216	48.818	<0.001
Residual			0.455		
Maximum gape duration (ms)	11.3 \pm 1.5	6.6 \pm 1.1	4.583	4.959	0.032
Residual			0.924		
Lower jaw elevation duration (ms)	27.6 \pm 2.9	14.9 \pm 1.9	15.339	23.886	<0.001
Residual			0.642		
Strike duration (ms)	122.9 \pm 15.3	38.8 \pm 3.2	19.740	36.970	<0.001
Residual			0.534		

Bold face shows significant results ($p < 0.01$ for body angle; $p < 0.05$ for all other variables) ($N = 20$; $df = 1, 38$).

Table 3. Principle component loadings of kinematic variables associated with aerial and aquatic feeding events in *Osteoglossum bicirrhosum*.

Variable	Factor 1	Factor 2
Strike duration (ms)	0.940	0.156
Time to maximum gape (ms)	0.904	0.074
Average attack velocity (SL s ⁻¹)	-0.875	0.123
Time to attack onset (ms)	0.819	-0.366
Maximum gape distance (cm)	-0.747	0.298
Lower jaw elevation duration (ms)	0.746	0.254
Body angle (degrees)	-0.676	0.030
Maximum gape duration (ms)	0.512	0.127
Attack duration (ms)	0.190	0.959
Percent of total variance explained	55.655	14.110

Bold face values indicate variables considered to load heavily on the respective component (loading scores $> |0.6|$) ($N = 4$).

Maximum gape is reached earlier and its extent is relatively greater in aerial than aquatic prey capture events (Table 2). In addition to the drag-reducing issues discussed above, this could be a behavioural modification intended to increase prey capture success. When objects are viewed from below the surface of the water at angles less than 90°, refraction results in a shift in the apparent position

of the object such that it appears higher than it actually is (Dill 1977, Timmermans 2001). Some species of fish, such as the archer fish, *Toxotes chatareus*, are able to account and behaviourally correct for this deviation in prey position (Timmermans 2001). However, *O. bicirrhosum* may lack this ability, as supported by the fact that we observed failed prey capture attempts in the aerial but not the aquatic presentation treatment. Observations of aerial feeding in the related freshwater butterflyfish, *Pantodon buchholzi*, suggest an inability to correct for refraction over study periods as long as 2 years (W. Saidel, personal communication). If *O. bicirrhosum* is similarly lacking in this ability, then the rapid, extensive mouth opening observed in our study could serve to minimize the targeting accuracy necessary to capture prey by maximizing the volume engulfed by the mouth. Assessment of the ability of *O. bicirrhosum* to correct for refraction is necessary to verify this postulate.

The use of non-elusive prey in the aquatic presentation treatment may have contributed to the comparably slow feeding kinematics in this study, as elusive prey have been found to elicit faster prey capture behaviour in other fishes

(Norton 1991, Nemeth 1997). However, during aquatic feeding in its natural habitat *O. bicirrhosum* chiefly takes inanimate or non-elusive terrestrial beetles and spiders at or near the surface of the water (Goulding 1980), likely expending little effort in pursuit. This suggests that the relatively long duration of aquatic as compared to aerial feeding kinematics is natural and that it is not simply an artifact of our experimental presentation.

During aerial feeding events, fish contracted their bodies to a larger extent and depressed their pectoral fins at a greater angular velocity than in aquatic feeding events. The exaggeration of these motions during leaping allows *O. bicirrhosum* to generate higher average attack velocities during aerial feeding events (Table 2). S-start postures such as those observed for *O. bicirrhosum* are typical during attacks executed by ambush predators like esocid and belonid fishes (Webb 1984, Porter & Motta 2000). The morphology of *O. bicirrhosum* is well suited for high-amplitude 'S' postures because it is elongate, flexible, laterally compressed, and dorsoventrally expanded by the presence of large anal and second dorsal fins (Webb 1984). These expanded fins contribute to the 'double tail' effect (Weihs 1989) by providing a relatively continuous body depth through the posterior region of this fish, allowing additional propulsive force to be generated by the tail. To attain the altitude necessary to capture aerial prey, the additional force generated by the body and fins must translate into upward motion, which is reflected in the greater body angle ($\sim 18^\circ$) in these as compared to aquatic feeding events (1.5°). Because prey height for aerial feeding events was kept relatively constant with respect to fish size in this study, the performance of *O. bicirrhosum* when prey height varies cannot be evaluated.

Osteoglossum bicirrhosum utilizes the distinctive leaping behaviour exhibited in this study to consume a prey base that is unavailable to most other fishes in the Amazon River basin. During the dry season, *O. bicirrhosum* is found in relatively small numbers (3.5% relative abundance) in floodplain lakes (Tejerina-Garro et al. 1998), where it occupies the littoral regions. Seasonal inundation of the Amazon forest can last between 3 and 11 months, increasing the mean water level of the Amazon River by as much as 10 m. This

generates a floodplain forest 70 000 km² in area, or approximately 1% of the total area of the Brazilian Amazon (Saint-Paul et al. 2000), and markedly increases habitat resources (Galacatos et al. 2004). During the wet season many fishes, including *O. bicirrhosum*, migrate into the inundated forest (Goulding 1980, Saint-Paul et al. 2000). During the temporally extensive wet season *O. bicirrhosum* occupies both the littoral regions of floodplain lakes and the inundated forest (Saint-Paul et al. 2000). While hunting along vegetated shores and under the forest canopy *O. bicirrhosum* feeds on a variety of small organisms either by leaping from the water to strip them from overhanging foliage, or by capturing them as they float on the surface of the water. Use of the versatile aerial prey capture behaviour characterized by rapid, extensive cranial kinematics, delayed onset of mouth opening, and dynamic pectoral and body-caudal fin propulsion allows *O. bicirrhosum* to exploit the terrestrial food base during this period when the aquatic food base is highly dispersed (Winemiller & Adite 1997), potentially conferring a competitive advantage over other fish species.

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