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Evaluating the use of ram and suction during prey capture by cichlid fishes

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Summary

We characterized prey-capture strategies in seven species of cichlid fishes representing diverse trophic habits and anticipated feeding abilities. The species examined were *Petenia splendida*, *Cichla ocellaris*, *Cichlasoma minckleyi*, *Astronotus ocellatus*, *Crenicichla geayi*, *Heros severus* (formerly *Cichlasoma severum*) and *Cyprichromis leptosoma*. Three individuals per species were filmed with video at 500 Hz as they captured live adult *Artemia* sp. and *Poecilia reticulata*. For each feeding sequence, we measured the contribution of predator movement towards the prey (i.e. ram) and the movement of prey towards the predator due to suction. The use of ram differed significantly among prey types and predator species, varying as much as sixfold across predator species. High values of ram resulted in high attack velocities. Jaw protrusion contributed as much as 50 % to overall ram values in some species, verifying its role in enhancing attack velocity. Suction distance did not vary significantly among species. Diversity in prey-capture behavior was therefore found to reflect differences among species in the strategy used to approach prey. Limited variation in the distance from which prey were sucked into the mouth is interpreted as the result of an expected exponential decline in water velocity with distance from the mouth of the suction-feeding predator. We propose that this relationship represents a major constraint on the distance over which suction feeding is effective for all aquatic-feeding predators.

Key words: ram–suction, index, prey capture, feeding, cichlid, feeding performance.

Introduction

One of the keys to interpreting physiological and biomechanical diversity is being able to relate functional design to whole-organism performance. Some areas of vertebrate biology have enjoyed considerable success in identifying measures of performance that link whole-animal abilities with morphological and physiological differences among species. For example, studies of locomotion often focus on sprint speed, endurance or efficiency (Jayne and Bennett, 1990; Garland, 1999; Aerts et al., 2000b). These measures of performance are readily compared across individuals and across species and have been important benchmarks in past research designed to understand the functional basis of locomotor diversity (Garland, 1984; Norberg and Rayner, 1987; Losos, 1996; Walker and Westneat, 2000).

One type of behavior that has proved particularly challenging to characterize with measurements of whole-animal performance is fish suction feeding. Suction feeding is the mechanism most fish species use to capture prey in the relatively viscous and dense aquatic medium. Fish draw prey into their mouth using a flow of water generated by a rapid drop in buccal pressure created as the buccal cavity rapidly expands (Lauder, 1980; Van Leeuwen, 1984; Van Leeuwen and Muller, 1984; Lauder, 1985). When prey are overtaken during a predatory attack, forward movement of the body and jaws, frequently termed ‘ram’, is typically combined with suction (Alexander, 1969; Nyberg, 1971; Norton, 1991).

Suction-feeding performance may be thought of as involving two independent variables: (i) the total volume of water drawn into the buccal cavity, which is related to the magnitude of buccal expansion, and (ii) the velocity of water at any point in space, which is related to the rate of expansion of the buccal cavity and the size of the oral aperture (Muller et al., 1982; Van Leeuwen and Muller, 1984). Most approaches to measuring suction-feeding performance have focused on these effects of the predator on the water. Estimates of the volume change of the buccal cavity have been made from films of feeding fish (Van Leeuwen, 1984; Ferry-Graham, 1998) or from morphological measurements of specimens (Norton, 1995; Cook, 1996; De Visser and Barel, 1998). Expansion of the buccal cavity creates a drop in pressure inside the cavity that can be measured, and a number of authors have used the magnitude of the subambient pressure peak to indicate suction performance (Osse, 1969; Lauder, 1983; Van Leeuwen and Muller, 1983; Grubich and Wainwright, 1997; Nemeth, 1997a). Several studies have estimated the velocity of water flowing into the expanding buccal cavity, most often by

visualizing the motion of particles suspended in front of the feeding fish (Muller and Osse, 1984; Van Leeuwen, 1984; Lauder and Clark, 1984; Ferry-Graham and Lauder, 2001). Since the forces that move the prey increase with water velocity, the flow of water entering the mouth is potentially useful as a measure of suction-feeding performance. Suction pressure and water velocity are expected to be positively related since, for a given fish, it is expected that strikes generating greater suction pressure should induce higher water velocity and, thus, greater drag on the prey (Muller and Osse, 1984; Van Leeuwen and Muller, 1984).

The volume change of the buccal cavity, the buccal pressure and the induced water velocity are proximate measures of suction-feeding performance. They are measures of the mechanical effects of the fish feeding mechanism on the water. However, they do not evaluate the interaction between predator and prey, an important element of suction-feeding performance. Thus, an alternative approach to measuring performance in suction feeding, suggested initially by Norton and Brainerd (Norton and Brainerd, 1993), is to measure the influence of the predator on the prey by recording the distance that the prey is drawn towards the predator during the strike. This is an integrated measure of suction-feeding performance because this variable will be influenced by total volume of water drawn in, the buccal pressure and the induced water velocity as well as the timing of the strike relative to the position of the prey. In this paper, we adopt this latter measure of suction-feeding performance and evaluate it in a comparative study of the relationship between the use of ram and suction in predatory cichlids.

A recent paradigm in fish feeding functional morphology is that species differ in the relative emphasis that they place upon ram and suction in closing the distance between themselves and their prey. Further, this variation is believed to be a major axis of ecomorphological diversification with consequences for jaw size and shape and the mechanical design of the feeding apparatus (Liem, 1980; Norton and Brainerd, 1993; Norton, 1995; Wainwright and Richard, 1995). In the present study, we assess ram and suction performance in seven species of predatory cichlids that vary widely in their anticipated prey-capture abilities. We envision a two-dimensional ram–suction space within which the prey-capture strategies of fish predators have diversified (Fig. 1), and our primary purpose in this study was to explore the nature of the cichlid radiation into this space using a preliminary sample of seven species. We focus on three major questions. (i) Are there combinations of ram and suction that these cichlids do not display, or are all regions of this space occupied? (ii) Are ram and suction highly correlated or largely independent of each other at intra- and interspecific levels? (iii) Does the distance from which prey are drawn into the mouth appear to work well as a measure of suction-feeding performance?

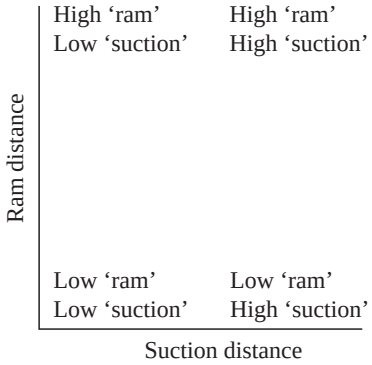

Fig. 1. The ram–suction space illustrating the potential combinations of predator movement towards the prey (ram distance) and suction-induced prey movement towards the predator (suction distance) used to close the distance between aquatic predator and prey. This study addresses the occupation of this feeding strategy space by seven species of cichlid fishes.

Materials and methods

The kinematics of prey capture was studied in seven cichlid species: *Petenia splendida* Guenther, *Cichla ocellaris* Schneider, *Cichlasoma minckleyi* Kornfield and Taylor, *Astronotus ocellatus* Agassiz, *Crenicichla geayi* Pellegrin, *Heros severus* Heckel (formerly *Cichlasoma severum*) and *Cyprichromis leptosoma* Scheuermann (Table 1; Fig. 2). All are native to Central and South America except *Cyprichromis*

Table 1. *Specimens and sample sizes used in the analyses*

Predator species	Standard length (cm)	Number of brine shrimp strikes	Number of guppy strikes
Petenia splendida	7.5	9	6
	7.6	6	7
	6.9	12	5
Cichla ocellaris	7.2	15	5
	7.8	15	4
	7.6	15	5
Astronotus ocellatus	6.6	13	5
	6.7	19	5
	6.5	15	4
Crenicichla geayi	8.8	16	4
	8.3	18	5
	7.6	15	4
Cichlasoma minckleyi	7.0	15	5
	6.9	13	6
	8.2	14	4
Heros severus	7.8	15	NA
	8.2	14	5
	8.8	13	NA
Cyprichromis leptosoma	5.4	14	4
	5.2	15	4
	4.2	12	NA

NA, not applicable.

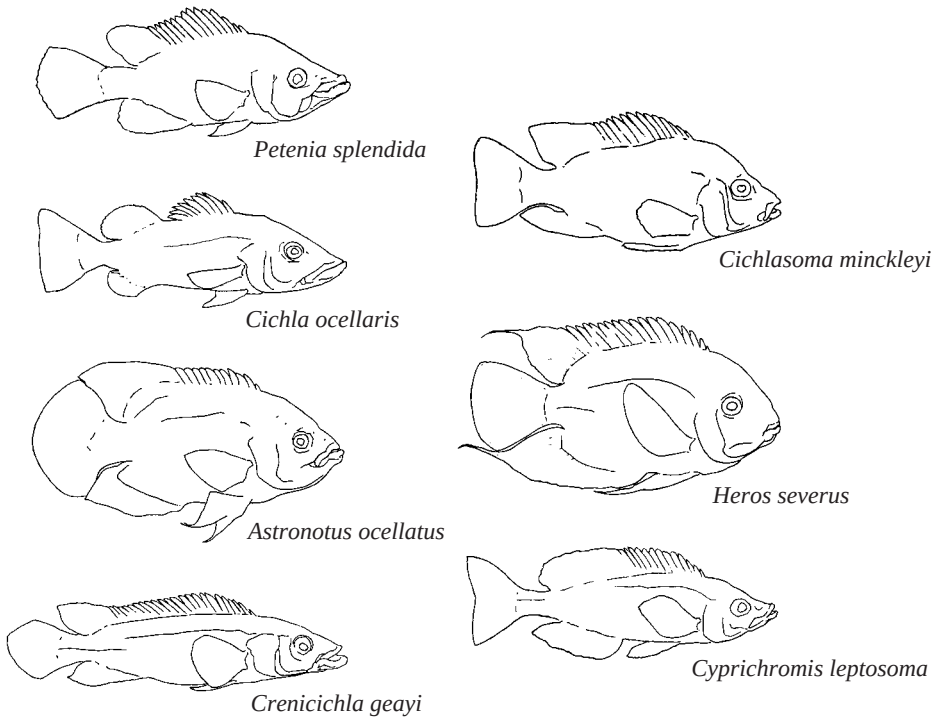

Fig. 2. Diagrams of the seven study species, illustrating overall patterns of body form. (A) *Petenia splendida*, (B) *Cichla ocellaris*, (C) *Astronotus ocellatus*, (D) *Crenicichla geayi*, (E) *Cichlasoma minckleyi*, (F) *Heros severus* and (G) *Cyprichromis leptosoma*. See Materials and methods for a discussion of the feeding biology of each species.

leptosoma, which is African. These species include some of the most piscivorous cichlids found in South America and other species that feed on much smaller, less active prey. Furthermore, we included *Cichla ocellaris* and *Heros severus* in this study because previous research has shown that they differ markedly in the ability to generate buccal pressure during prey capture (Norton and Brainerd, 1993). *Petenia splendida* is a lake-dwelling piscivore (Koenings, 1989; Conkel, 1993), with unusually protrusible jaws. *Cichla ocellaris* is a large-mouthed piscivore (Lowe-McConnell, 1969; Norton and Brainerd, 1993; Winemiller et al., 1997). *Astronotus ocellatus* feeds on aquatic insects and fishes (Winemiller, 1990). Like other member of the genus, *Crenicichla geayi* is an active predator of elusive arthropods and fishes (Lowe-McConnell, 1991; Sabino and Zuanon, 1998). There are two forms of *Cichlasoma minckleyi*; the diet of the papilliform morph that we studied is apparently more representative of the genus (Kornfield and Koehn, 1975; Liem and Kaufman, 1984) and is dominated by plant material (Kornfield et al., 1982) and benthic invertebrates (Lowe-McConnell, 1991; Conkel, 1993). *Heros severus* is associated with densely vegetated areas and feeds on small invertebrates and plant material (Lowe-McConnell, 1969; Merigoux et al., 1998). *Cyprichromis leptosoma* is an open-water zooplanktivore from Lake Tanganyika (Ribbink, 1991; Watanabe, 2000).

Three individuals of each species were filmed feeding on two prey types: living adult *Artemia* sp., or brine shrimp, a non-elusive but mobile prey, and live *Poecilia reticulata*, or guppies, a larger and more elusive prey. Individuals were housed and filmed at 27±2 °C in 100 l aquaria at the University of California, Davis. Video sequences were recorded at 500 images s^{-1} with a NAC Memrecam ci digital system with illumination from two or three 600 W flood lights. Distances in the images were scaled by recording an image of a ruler placed in the field of view with the same zoom factor used when recording feeding sequences. Fish were offered one or a few items of prey at a time and were allowed to feed until satiated. Filming generally occurred over a 3–5 day period for each individual.

To quantify movement of the prey and the predator, we analyzed images from the video sequences using NIH Image for Macintosh, Scion Image for PC or Didge for PC (A. Cullum, University of California Irvine). We determined the *x*,*y* coordinates of four landmarks at the onset of each sequence: (i) the anterior tip of the premaxilla (upper jaw); (ii) the anterior tip of the dentary (lower jaw); (iii) the anterior-most margin of the orbit (a reference point); and (iv) the estimated center of mass of the prey item. These landmarks were tracked through four discrete points in time: (i) the onset of slow mouth opening, defined as the time at which an opening movement of the lower jaw could be detected; (ii) the onset of fast mouth opening, defined as the frame prior to the one in which the mouth began to open rapidly; (iii) the time of peak gape, defined as the time at which the straight-line distance between the tips of the upper and lower jaws first reached its maximum; and (iv) the time of prey capture, defined as the frame immediately prior to the one in which the center of mass of the prey crossed the boundary formed by a line drawn between the tips of the open upper and lower jaws. Between 6 and 19 brine shrimp feeding sequences were analyzed from each individual. For the individuals that would eat guppies, four or five guppy sequences were analyzed (Table 1). We analyzed only sequences in which a lateral view of the

fish could clearly be seen in the image and the fish was perpendicular to the camera.

Changes in the positions of the four points were used to calculate several variables that characterized movements of the predator and prey. Each set of variables was calculated under two conditions: with the onset of slow mouth opening defined as time zero, t_0, and with the onset of fast mouth opening defined as t_0. The time of capture ($t_{capture}$) was determined relative to both measures of t_0, and the following displacement variables were calculated: (i) predator–prey distance, the distance between the predator and the prey at t_0; (ii) suction distance, the distance moved by the prey towards the predator from t_0 to $t_{capture}$ (note that this is often referred to as D_{prey}; Norton and Brainerd, 1993); (iii) ram distance (often referred to as $D_{predator}$), the distance moved towards the prey by the predator including the contribution of upper jaw protrusion, measured at the tip of the upper jaw, from t_0 to $t_{capture}$; (iv) ram distance$_{body}$, the distance moved towards the prey item by the predator's body, measured at the orbit, from t_0 to $t_{capture}$. Suction and ram variables were also used to calculate the ram–suction index (RSI; Norton and Brainerd, 1993): (suction distance minus ram distance)/(ram distance plus suction distance). In addition, we determined gape at prey capture, peak gape during the strike, jaw protrusion at prey capture and the time between $t_{capture}$ and $t_{peak\ gape}$.

A two-factor nested analysis of variance (ANOVA) was performed using Systat v. 9.0. Prey type and predator species were crossed factors, with individual nested within the predator species effect. A full model incorporating the interaction terms prey type × predator species and prey type × individual[predator species] was used. *F*-ratios were estimated according to Winer et al. (Winer et al., 1991) and were calculated as follows: the fixed factor predator species was tested over individual[predator species], the fixed factor prey type was tested over the interaction term prey type × individual[predator species], and the random factor individual[predator species] was tested over the error term. The prey type × predator species interaction was tested over the prey type × individual[predator species] interaction, and the prey type × individual[predator species] interaction was tested over the error term. Significant predator species effects were further investigated using Fisher's protected least significant difference *post-hoc* analysis (PLSD). Dependent variables used in this model were suction distance, ram distance and ram distance$_{body}$. The analysis was performed for these variables estimated from both slow mouth opening (SO) and fast mouth opening (FO) to determine whether these differences in the calculations affected interpretation of the results. This same analysis was used to compare gape among species, which did not vary with SO or FO. *P*-values were adjusted table-wise for multiple tests (following Rice, 1989).

Individuals for which both brine shrimp and guppy strikes could not be obtained were dropped from the global analysis described above. This resulted in one *Cyprichromis leptosoma* being removed from the analysis and *Heros severus* being removed altogether since only one individual of that species was able to capture both prey types. To determine how *Heros severus* compared with the other species, univariate ANOVAs were performed for the variables identified above for strikes on brine shrimp prey. All three *Cyprichromis leptosoma* were also included in this analysis. This model was a one-factor nested ANOVA with species as the main effect and individual nested within species. The species effect was tested over the nested term. To determine whether guppy strikes differed from brine shrimp strikes within *Heros severus*, a *t*-test was performed comparing strikes on the two prey types for the individual that consumed both. In these tests, *P*-values were also adjusted according to Rice (Rice, 1989).

Given significant individual effects in the two ANOVA analyses, general trends within individuals and species were also investigated using regression analysis. Trends among species, such as effects of body size on the dependent variables quantified and the relationship between suction distance and gape, were also investigated using regression analysis on means for each individual. To explore the extent to which ram and suction distance varied independently in the ram–suction space (Fig. 1), correlations were calculated for each prey type across all feeding sequences in each species.

Results

During video recording sessions, fish typically responded to the presence of food by orienting their body towards the prey, followed by an approach phase and finally a strike. At the onset of the strike, the jaws began to open slowly. This was followed by a distinct increase in the rate of mouth opening signifying the onset of fast mouth opening (Fig. 3). The jaws were rapidly opened to peak gape and often protruded towards the prey as the predator continued towards the prey item (Fig. 3; Table 2). As the predator approached, the prey item moved into the buccal cavity, presumably because it was entrained in a flow of water being generated by the expanding buccal cavity (Table 3, suction distance). The timing of peak gape was variable, occurring both prior to and after $t_{capture}$ (Table 2), and was typically maintained until after the prey disappeared from view inside the mouth. Following capture, the jaws were returned to their relaxed, pre-feeding position.

Gape at $t_{capture}$ differed among predator species (F=9.75; d.f.=5,11; P=0.0007), with *Cichla ocellaris* exhibiting a significantly larger gape than that of all other species at around 1 cm (all P<0.01), and *Cyprichromis leptosoma* producing a 0.4 cm gape that was significantly smaller than that of all other species (all P<0.03). Guppies elicited wider gapes than did brine shrimp (F=21.7; d.f.=5,11; P=0.0006), with notable increases of approximately 0.3–0.4 cm seen in *Petenia splendida*, *Cichla ocellaris* and *Crenicichla geayi* (Table 2).

Suction distance and ram distance values calculated from slow opening (results not shown) gave consistently larger values than from fast opening (Table 3). None of our statistical analyses detected a species or prey type effect on suction or ram distance when these variables were estimated from slow opening (all P>0.08).

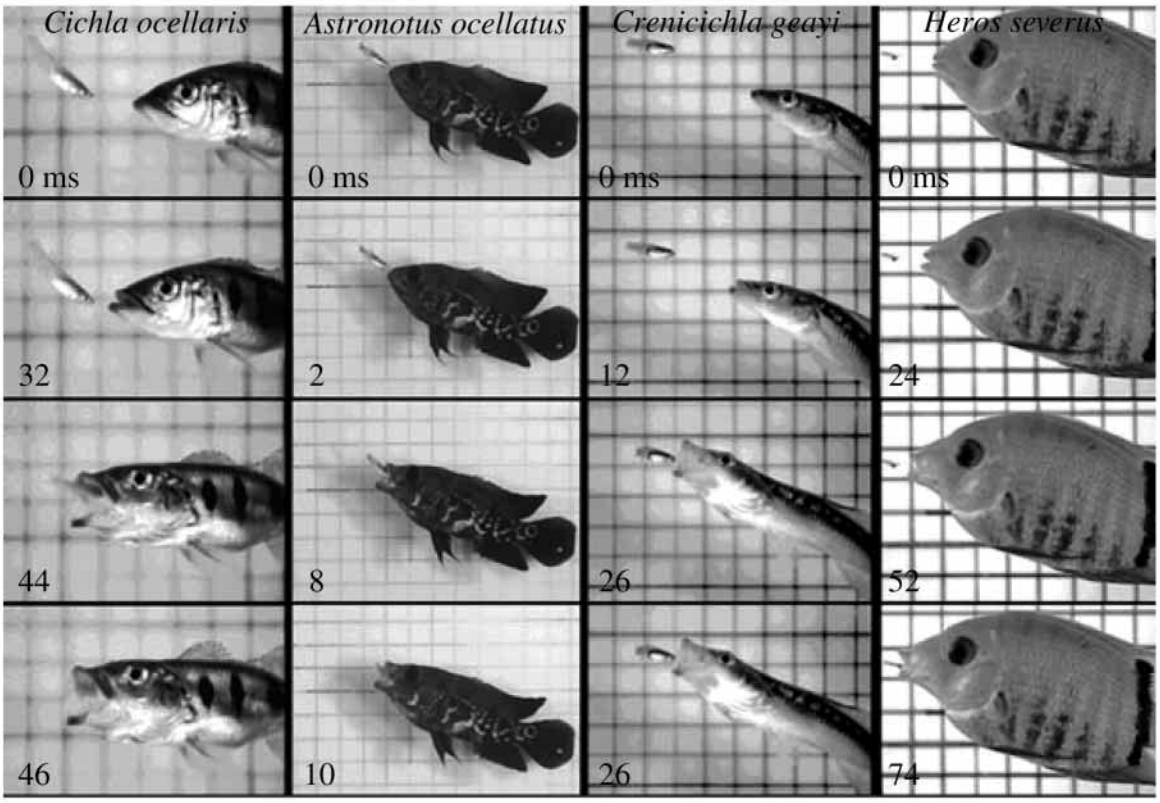

Fig. 3. Sample sequences from prey capture sequences captured on video. The four frames analyzed in each sequence are illustrated: onset of slow mouth opening, onset of fast mouth opening, peak gape distance and time of prey capture. Times shown (ms) were calculated relative to the onset of slow mouth opening. The background is a grid of 1 cm squares.

Table 2. *Kinematic displacement variables of seven cichlid species feeding on brine shrimp and guppies*

		Brine shrimp prey		
Predator	*SL* (cm)	Gape at $t_{capture}$ (cm)	Peak gape (cm)	$t_{capture}$ to $t_{peak\ gape}$* (s)
Petenia splendida	7.3±0.2	0.751±0.097	0.804±0.098	0.003
Cichla ocellaris	7.5±0.2	1.106±0.025	1.168±0.036	0.003
Astronotus ocellatus	6.6±0.1	0.654±0.097	0.852±0.066	–0.011
Crenicichla geayi	8.2±0.3	0.629±0.060	0.722±0.070	0.009
Cichlasoma minckleyi	7.4±0.4	0.647±0.084	0.664±0.073	0.000
Heros severus	8.3±0.3	0.765±0.087	0.786±0.073	–0.0003
Cyprichromis leptosoma	4.9±0.4	0.398±0.009	0.416±0.010	0.002
		Guppy prey		
Predator	*SL* (cm)	Gape at $t_{capture}$ (cm)	Peak gape (cm)	$t_{capture}$ to $t_{peak\ gape}$* (s)
Petenia splendida	7.3±0.2	1.125±0.077	1.214±0.035	0.004
Cichla ocellaris	7.5±0.2	1.393±0.140	1.428±0.152	0.003
Astronotus ocellatus	6.6±0.1	0.731±0.351	0.950±0.111	0
Crenicichla geayi	8.2±0.3	1.022±0.083	1.078±0.083	0.0025
Cichlasoma minckleyi	7.4±0.4	0.761±0.100	0.818±0.077	0.003
Heros severus	8.8 (NA)	0.725 (NA)	0.767 (NA)	–0.002
Cyprichromis leptosoma	5.3±0.1	0.380±0.018	0.378±0.066	–0.010

Values are means of the three individual means (±S.E.M.).
*Filming at 500 frames s^{-1} provided a resolution of 0.002 s; negative values indicate that peak gape occurred before prey capture.
SL, standard length; $t_{capture}$, time of capture; $t_{peak\ gape}$, time of peak gape; NA, not applicable.

Table 3. *Kinematic variables estimated from the time and position of the predator at the onset of fast mouth opening*

		Brine shrimp prey					
Predator	*SL* (cm)	$t_{capture}$ (s)	Predator–prey distance (cm)	Suction distance (cm)	Ram $distance_{body}$ (cm)	Ram distance (cm)	RSI
Petenia splendida	7.3±0.2	0.030±0.006	1.08±0.08	0.15±0.02	0.62±0.14	0.98±0.12	0.73±0.04
Cichla ocellaris	7.5±0.2	0.019±0.003	1.11±0.09	0.28±0.03	0.63±0.09	0.99±0.10	0.56±0.01
Astronotus ocellatus	6.6±0.1	0.028±0.004	0.80±0.05	0.26±0.04	0.33±0.04	0.49±0.06	0.32±0.03
Crenicichla geayi	8.2±0.3	0.025±0.007	1.03±0.19	0.22±0.07	0.61±0.19	0.81±0.23	0.53±0.06
Cichlasoma minckleyi	7.4±0.4	0.044±0.004	0.93±0.20	0.21±0.04	0.46±0.18	0.70±0.21	0.45±0.14
Heros severus	8.3±0.3	0.042±0.008	1.08±0.13	0.27±0.06	0.46±0.12	0.78±0.14	0.46±0.15
Cyprichromis leptosoma	4.9±0.4	0.013±0.001	0.57±0.15	0.20±0.05	0.20±0.09	0.47±0.14	0.35±0.13
		Guppy prey					
Predator	*SL* (cm)	$t_{capture}$ (s)	Predator–prey distance (cm)	Suction distance (cm)	Ram $distance_{body}$ (cm)	Ram distance (cm)	RSI
Petenia splendida	7.3±0.2	0.018±0.005	1.86±0.34	0.15±0.06	0.89±0.29	1.86±0.48	0.85±0.03
Cichla ocellaris	7.5±0.2	0.013±0.001	1.51±0.23	0.31±0.12	1.10±0.18	1.49±0.23	0.66±0.12
Astronotus ocellatus	6.6±0.1	0.010±0.002	1.04±0.11	0.25±0.07	0.50±0.10	0.84±0.18	0.54±0.09
Crenicichla geayi	8.2±0.3	0.016±0.005	1.70±0.24	0.26±0.10	1.17±0.29	1.51±0.33	0.73±0.05
Cichlasoma minckleyi	7.4±0.4	0.030±0.007	0.83±0.19	0.26±0.02	0.40±0.15	0.73±0.19	0.43±0.12
Heros severus	8.8 (NA)	0.008 (NA)	0.78 (NA)	0.19 (NA)	0.11 (NA)	0.40 (NA)	0.47 (NA)
Cyprichromis leptosoma	5.3±0.1	0.011±0.004	0.42±0.13	0.23±0.07	0.12±0.05	0.30±0.02	0.16±0.13

Values are means of the three individual means (±S.E.M.).
RSI, ram–suction index; *SL*, standard length; $t_{capture}$, time of capture; NA, not applicable.

Significant main effects of the ANOVA were detected for some of the variables estimated from fast opening and, henceforth, we refer only to results using fast opening as the reference time (Table 4). Ram distance differed among predator species (F=3.16; d.f.=5,11; P=0.03) and between prey types (F=12.80; d.f.=1,11; P=0.003). For brine shrimp feedings, the rank order of species means for ram distance and ram $distance_{body}$ were the same (Table 4), although the contribution of jaw protrusion caused almost a doubling of ram for most species. The greatest increase was seen in *Petenia splendida* feeding on guppy prey, which had the highest ram distance at 1.86 cm (Table 3). Ram $distance_{body}$ differed among predator species (F=3.16; d.f.=5,11; P=0.05; Table 4) and between prey types (F=12.80; d.f.=1,11; P=0.004; Fig. 4). *Post-hoc* tests indicated that *Petenia splendida*, *Cichla ocellaris* and *Crenicichla geayi* had significantly larger values of ram $distance_{body}$ than the other species (all P<0.05; Table 4). However, a significant prey type effect suggests that the magnitude of this result differed between prey. Although the predator species × prey type interaction term was not significant (Table 4), a fairly large change across prey type in ram distance was seen only in *Petenia splendida*, *Cichla ocellaris* and *Crenicichla geayi*. In addition, guppies consistently elicited a larger ram distance in *Petenia splendida*, *Cichla ocellaris*, *Astronotus ocellatus* and *Crenicichla geayi*, while a smaller ram distance was elicited in *Cichlasoma minckleyi*, *Heros severus* and *Cyprichromis leptosoma* (Fig. 5).

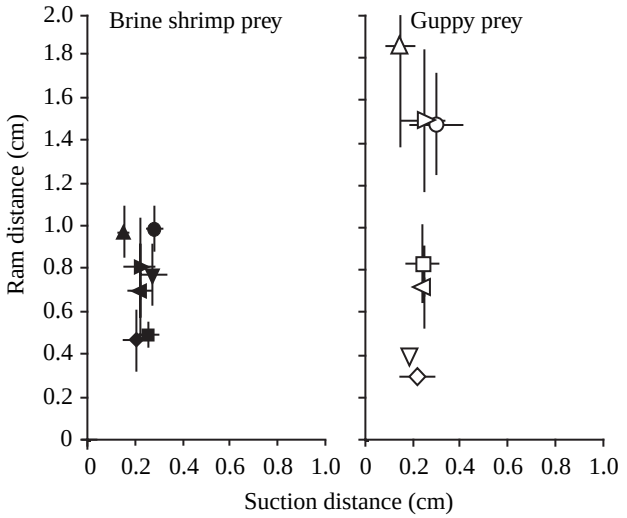

Fig. 4. Mean and standard errors for the seven cichlid species in the ram–suction space. Note that species varied more in ram distance than in suction distance and that the latter never exceeded 0.5 cm. All variables are calculated from the onset of fast mouth opening (see text for details). Species are as follows: (▲) *Petenia splendida*; (●) *Cichla ocellaris*; (■) *Astronotus ocellatus*; (►) *Crenicichla geayi*; (◄) *Cichlasoma minckleyi*; (▼) *Heros severus*; (◆) *Cyprichromis leptosoma*. Filled symbols indicate strikes on brine shrimp and open symbols indicate strikes on guppies.

Table 4. *Statistical results from the main effects of the global ANOVA and* post-hoc *tests for suction and ram distance measured relative to onset of fast opening*

	Predator species effect		Prey type effect		Predator×Prey interaction	
Dependent variable	*F* (d.f.=5,11)	*P*	*F* (d.f.=1,11)	*P*	*F* (d.f.=5,11)	*P*
Suction distance	0.827	0.56	0.726	0.41	0.055	0.98
Ram distance$_{body}$	3.156	0.05*,[1]	12.80	0.004*	2.110	0.14
Ram distance	3.748	0.03*,[2]	14.59	0.003*	1.907	0.17

*Significant at P=0.05 level after correction.

[1]*Post-hoc* results for ram distance$_{body}$. Lines connect species that do not differ from one another in *post-hoc* comparisons of target species against the others. The top line indicates comparisons of *Cg* with other species, the second line *Co* to other species and so on.

Cg *Co* *Ps* *(Hs)* *Cm* *Ao* *Cl*

[2]*Post-hoc* results for ram distance. Explanation for *post-hoc* comparison results as in footnote 1.

Ps *Cg* *Co* *(Hs)* *Cm* *Ao* *Cl*

Ps, *Peteria splendida*; *Cg*, *Crenicichla geayi*; *Co*, *Cichla ocellaris*; *Hs*, *Heros severus*; *Cm*, *Cichlasoma minckleyi*; *Ao*, *Astronotus ocellatus*; *Cl*, *Cyprichromus leptosoma*.

In the global analysis, suction distance did not vary among species or prey type (Table 4; all P>0.41; Fig. 4), nor was a relationship detected between suction distance and gape at $t_{capture}$ (P=0.28 for brine shrimp, P=0.65 for guppy). A trend among species did exist, however, because mean suction distance varied by approximately twofold across species for both guppy and brine shrimp data (Table 3). For guppy feedings, the lowest suction distance was seen in *Petenia splendida*, at 0.15 cm, and the highest in *Cichla ocellaris*, at 0.31 cm. Mean RSI values ranged between 0.16 and 0.85 (Table 3) and, because suction distance varied over a smaller range than ram distance, RSI was influenced mostly by differences among species in ram distance. As an indication of this, we note that the RSI was not significantly related to suction distance (F=0.11, d.f.=1,5; P=0.76). Mean ram distance per species was positively associated with gape distance at $t_{capture}$ for both prey types (for brine shrimp, P=0.04; for guppy, P=0.016; Fig. 6). Fish standard length did not significantly affect either ram or suction distance (Fig. 7; all P>0.6). Significant variation among individuals was detected in all models reported in Table 4.

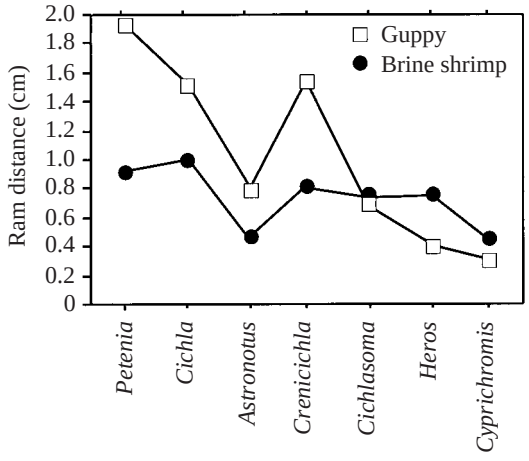

Fig. 5. The effect of prey type on ram distance. Species that feed on larger, more active prey in the wild (i.e. *Petenia splendida*, *Cichla ocellaris*, *Crenicichla geayi*) showed the greatest increase in ram distance when feeding on guppies, while predators of zooplankton and small insects (i.e. *Cichlasoma minckleyi*, *Heros severus*, *Cyprichromis leptosoma*) showed no prey effect or even a reversal of the trend.

Ram and suction distance were only significantly correlated within *Crenicichla geayi* strikes on brine shrimp, although most values indicated a weakly positive relationship in which feeding sequences with a high ram distance also tended to have higher values of suction distance (Table 5; Fig. 8). There were no cases of significant negative correlations, although some values showed this trend (e.g.

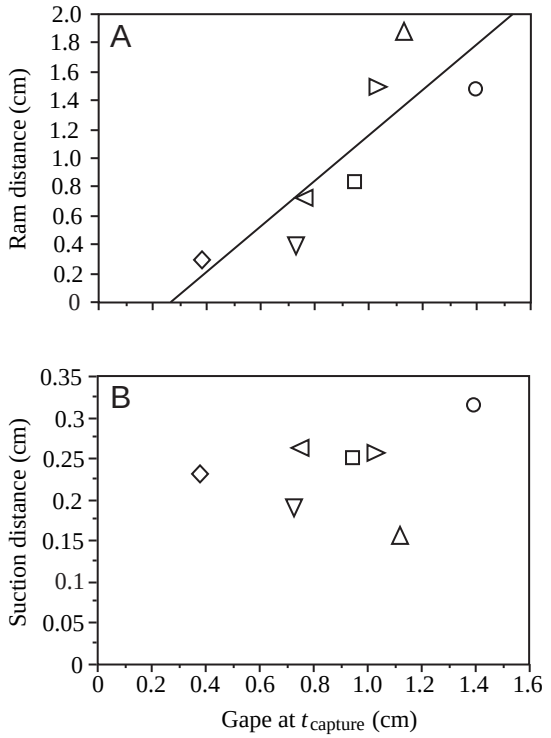

Fig. 6. Relationships between (A) ram and (B) suction distance and mouth diameter (gape at $t_{capture}$) when feeding on guppies. Values are means for each species in the study. The regression between ram distance (r^2=0.72, P=0.016) and gape distance is significant, but that between suction distance and gape distance is not (r^2=0.06, P=0.65). Species are as follows: (△) *Petenia splendida*; (○) *Cichla ocellaris*; (□) *Astronotus ocellatus*; (▷) *Crenicichla geayi*; (◁) *Cichlasoma minckleyi*; (▽) *Heros severus*; (◇) *Cyprichromis leptosoma*.

Table 5. *Correlations between ram distance and suction distance for each species feeding on the two prey*

Cichlid taxon	Brine shrimp prey	Guppy prey
Petenia splendida	0.36	0.55
Cichla ocellaris	0.31	0.04
Astronotus ocellatus	0.13	0.56
Crenicichla geayi	0.47*	0.58
Cichlasoma minckleyi	–0.22	–0.01
Heros severus	0.02	0.92
Cyprichromis leprosoma	–0.13	0.59

*P<0.05 with the sequential Bonferroni correction of Rice (Rice, 1989).

Cyprichromis leptosoma and *Cichlasoma minckleyi* feeding on brine shrimp).

The regression of species means of ram distance on mean attack velocity was not significant for brine shrimp feedings (P>0.28), but was significant for guppy feedings (Fig. 9; r^2=0.76; P=0.011). Ram distance was not significantly related to $t_{capture}$ (P>0.28).

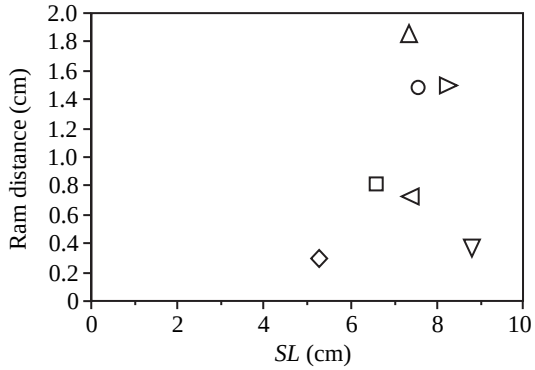

Fig. 7. Scaling of ram distance with fish standard length (*SL*). The relationship between ram distance and *SL* is not significant (r^2=0.04, P=0.68). The relationship between suction distance and *SL* (not shown) was also not significant (r^2=0.006; P=0.77). Species are as follows: (△) *Petenia splendida*; (○) *Cichla ocellaris*; (□) *Astronotus ocellatus*; (▷) *Crenicichla geayi*; (◁) *Cichlasoma minckleyi*; (▽) *Heros severus*; (◇) *Cyprichromis leptosoma*.

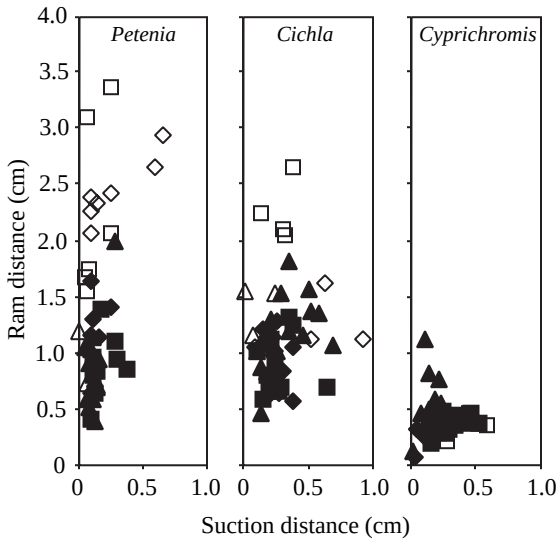

Fig. 8. Samples of the complete ram and suction distance data for three cichlid species: *Petenia splendida*, *Cichla ocellaris* and *Cyprichromis leptosoma*. Different symbols refer to the different individuals in each plot. Filled symbols represent strikes on brine shrimp prey, and open symbols represent strikes on guppy prey. Note that the far right-hand region of the potential ram–suction space is not occupied by any species and that the peak values of suction distance never exceeded 1.0 cm.

Discussion

The seven taxa included in this study did not differ in suction distance. This result is surprising given that these species were selected to represent a broad diversity of feeding strategies found within the Cichlidae. However, the species did show considerable variation in the role of their movement towards the prey during the strike. Mean ram distance ranged sixfold across species when feeding on the more elusive guppies (Table 3, Table 4). Thus, we find that cichlids vary

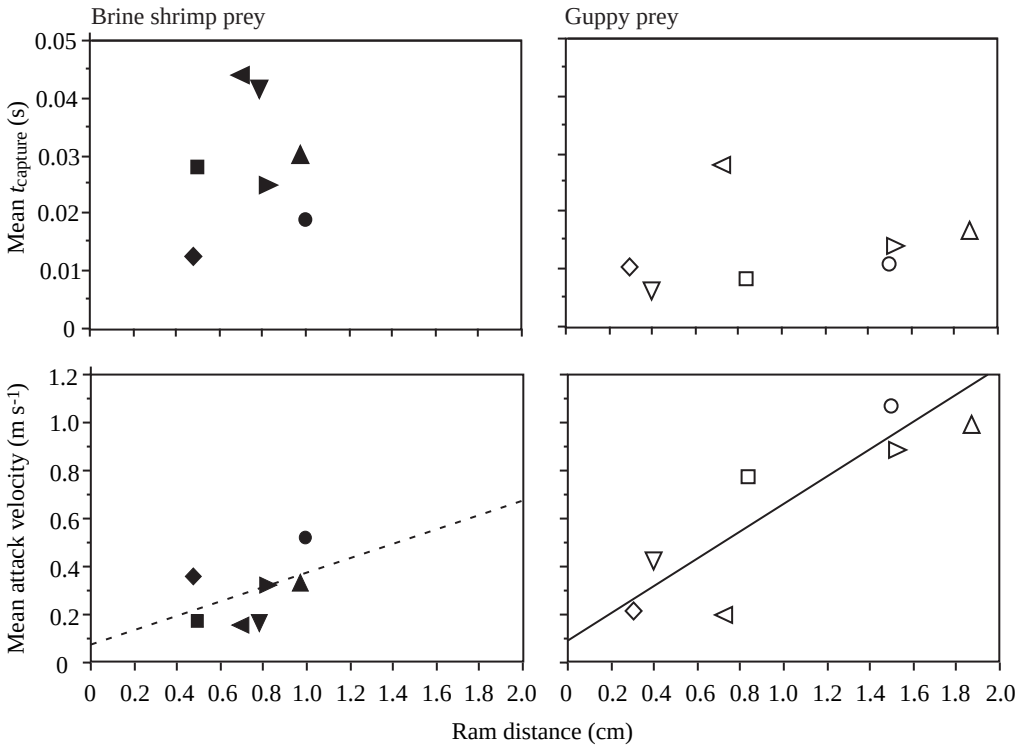

Fig. 9. Relationship between mean ram distance and mean attack velocity in seven cichlid species feeding on guppies and brine shrimp. Points plotted are the means for each species. Attack velocity was calculated as ram distance divided by time of capture ($t_{capture}$; measured from fast mouth opening). Although species differ in $t_{capture}$, a significant effect of ram distance on attack velocity for guppy prey (r^2=0.76, P=0.011) is caused by variation in ram distance (for brine shrimp, P>0.05). There is no relationship between ram distance and $t_{capture}$ (P=0.28). Species are as follows: (▲) *Petenia splendida*; (●) *Cichla ocellaris*; (■) *Astronotus ocellatus*; (►) *Crenicichla geayi*; (◄) *Cichlasoma minckleyi*; (▼) *Heros severus*; (◆) *Cyprichromis leptosoma*. Filled symbols indicate strikes on brine shrimp and open symbols indicate strikes on guppies.

considerably in their prey-capture strategies, but that this variation lies primarily along the ram axis, with less variation in the distance from which they draw in prey (Fig. 4).

The lack of significant interspecific variation in suction distance reveals a layer of unexpected conservation in the suction-feeding mechanics of cichlid fishes. Our result is especially striking in the light of previous findings that *Heros severus* exhibits approximately twice the buccal pressure of *Cichla ocellaris* during feeding on elusive prey, suggesting that *Heros severus* should have greater suction distance values (Norton and Brainerd, 1993). In our study, *Cichla ocellaris* had higher values of suction distance with both prey types (Table 3), although these differences were never significantly different from those found for other species. The previously described difference in the ability to generate suction pressure fits a general expectation that small-mouthed species will generate greater pressure gradients than related taxa with larger mouths (Muller and Osse, 1984; Norton, 1991; Norton and Brainerd, 1993). If the volume and rate of buccal expansion are held constant, fish that draw water through a smaller oral aperture would be expected to generate greater values of subambient pressure and a higher velocity of water flow into the mouth. A greater velocity of water at the mouth opening should result in the ability to draw prey from further away (Muller and Osse, 1984). Our study provides surprisingly little support for this expectation.

Comparative data on interspecific variation in suction distance are sparse in the literature. In the past decade, researchers reporting studies of suction distance and ram distance have typically not reported the separate measurements, but rather combine them into the ram–suction index (Norton and Brainerd, 1993). However, a recent study of butterflyfishes found no significant difference in suction distance among five species thought to differ considerably in suction-feeding ability. There was also a significant difference among species in ram distance (Ferry-Graham et al., 2001). Data presented on individual feeding sequences by Norton and Brainerd indicate minor differences between their study species in suction distance (see fig. 5 in Norton and Brainerd, 1993). We are unaware of any direct observations of large differences in suction distance among similarly sized fish species feeding on similar prey.

We propose two possible explanations for why suction distance showed such small variation among species. First, it is possible that the fish species in this study do differ in the distance from which they can draw a common prey type into their mouth, but that they did not express this ability. Our experimental protocol may not have caused these fish to exhibit their maximal capacity for this trait. Individual fish ultimately control suction distance by the timing of their suction-feeding effort relative to the position of the prey item. Variation among

species in buccal pressure and induced water velocity will only result in differences in suction distance if fishes attempt to extend the distance from which they draw prey.

Second, theoretical relationships derived from non-steady fluid mechanics suggest that variation in suction pressure and induced water velocity at the mouth opening may not translate into significant changes in water velocity away from the mouth. Water is drawn into the mouth during suction feeding in response to the subambient pressure generated inside the buccal cavity. Water flowing through the mouth opening is drawn from a space in front of the mouth as well as from above and below the head (Alexander, 1967; Weihs, 1980; Van Leeuwen, 1984; Lauder and Clark, 1984), although the rate of flow towards the mouth will not be the same from all directions (Weihs, 1980; Muller et al., 1982). The velocity of any given water particle will be inversely proportional to d^3 (Muller et al., 1982), where d is the distance of the particle from the center of the mouth. This relationship implies that water velocity, and thus the forces that determine the ability of the fish to draw prey into the mouth, drop off precipitously with distance from the mouth. Because water velocity decays exponentially with distance from the mouth aperture, even a doubling of the water velocity at the mouth may do little to extend the distance from which prey can be drawn in. An interesting consequence of this relationship is that, although variation in subambient pressure that is created may result in substantial variation in the velocity of water at the mouth opening, the effect on water velocity as one moves away from the oral opening will be small. This mechanical phenomenon may represent a major constraint on the distance over which suction feeding can be expected to be effective in aquatic-feeding vertebrates.

We emphasize that, although suction distance may not scale linearly with water velocity at the oral aperture, a positive relationship is expected. Greater water velocity at the mouth should result in a greater potential suction distance. However, suction distance will vary on a much smaller scale than velocity at the mouth opening. Our interpretation of the diversity of feeding performance in cichlids is that variation among species may exist in the capacity to produce pressure and water velocity at the mouth aperture, but that this variation is compressed when it is transformed into measures of suction distance because of the exponential decline in velocity with distance from the mouth.

Re-evaluating the role of ram and suction in aquatic feeding strategies

Movement of the predator towards the prey, termed ram, and movement of the prey towards the predator due to suction have been widely recognized as distinct but synergistic elements of prey capture in fishes (Alexander, 1967; Nyberg, 1971; Liem, 1980; Motta, 1984; Van Leeuwen and Muller, 1984; Norton and Brainerd, 1993). In recent years, the predominant picture that has emerged is that ram and suction represent extremes of a continuum from pure ram to pure suction, with most strike sequences and most fish species utilizing a combination of these actions to capture mobile prey (Norton and Brainerd, 1993; Wainwright and Richard, 1995). Our findings suggest that a modified interpretation of the role of ram and suction in fish feeding is needed.

In contrast to expectations derived from their feeding ecology and from previous studies of functional morphology, we found no significant differences among species in suction distance. Thus, variation in strike distance is formed mostly by changes in predator distance (Fig. 4). With reference to the potential space of ram and suction illustrated in Fig. 1, we found that the right-hand side of this graph was unoccupied, and species instead varied primarily along the ram axis. Even within species, ram and suction distance were only weakly correlated across feeding trials with a single prey type (Table 5). Thus, both among species and within individual fishes, ram and suction distance were usually unrelated. We suggest that the ram–suction continuum is better thought of as a two-dimensional space than a single axis.

If, as discussed in the previous section, there are severe mechanical limits on how far fish can extend suction distance by altering buccal pressure, then we predict that a low interspecific range in this variable will prove to be a general feature of fish prey-capture strategies. Assuming that, for an individual fish, suction is effective only over a limited distance, a key component of the strategy to capture an elusive prey item is the mechanism used to get close enough to the prey so that suction can be employed successfully. When capturing elusive guppies, species in this study varied along an axis that, at one extreme, employed high attack velocities during the strike and, at the other extreme, relied on stealth to approach the prey prior to the strike (Fig. 9). Taxa such as *Petenia splendida*, *Cichla ocellaris* and *Crenicichla geayi* that employ high amounts of ram achieve higher attack velocities than taxa such as *Cyprichromis leptosoma* and *Heros severus* that approached the prey more slowly prior to the strike (Fig. 9).

We advocate a view in which the primary role of ram is to move the mouth opening rapidly close enough to the prey to permit the successful use of suction. An extreme or very rapid ram strategy can be expected to be most important when feeding on elusive prey that have the greatest capacity for detecting the predator and escaping the flow of water created by suction. As noted by other authors (Norton, 1991; Nemeth, 1997b), we found that ram tended to increase within cichlid species when feeding on the more elusive guppies (Fig. 4), and those species in our study known to feed on more elusive prey in the wild, *Petenia splendida*, *Cichla ocellaris* and *Crenicichla geayi*, were the taxa that used the greatest amount of ram (Fig. 4). In the species we studied, ram was achieved by a combination of forward body movement and jaw protrusion (Fig. 4). The proportional effect of jaw protrusion was considerable in some cases, particularly for *Petenia splendida* and *Heros severus*, in which ram distance was nearly doubled by jaw protrusion (Table 3). Jaw protrusion contributes to the ram component of a strike and in this study increased attack velocity (Fig. 9; see also Alexander, 1969; Motta, 1984).

If variation among taxa in the ability to generate pressure

gradients does not translate into substantial differences in suction distance, what are the possible performance advantages of increased buccal pressure? We see at least two ways in which increased buccal pressure may enhance suction-feeding performance. First, a general relationship can be expected in which strikes with greater buccal pressure generate a greater velocity of water flow at the mouth opening, and in close proximity to the mouth, than strikes with smaller pressure gradients. This enhanced velocity of water flow should result in a greater ability to accelerate prey into the mouth because the drag forces that are generated will increase exponentially with water velocity. Thus, although the flow may not extend very far in front of the mouth, greater rates of flow near the mouth can be expected to enhance prey-capture performance. Second, enhanced suction pressure and the resulting enhanced flow velocity may be especially important in a common feeding behavior that is not dealt with in the present paper. Many fish use suction to capture prey that are either perched on structures or even attached firmly to a substratum (Drucker and Jensen, 1991; Norton, 1991; Norton, 1995). In these situations, the high flow rates that are generated close to the mouth may be especially important in helping to dislodge prey. The use of high-velocity suction feeding to capture prey that grip structures in the environment may be more common and more significant in the diversification of teleost feeding mechanisms than previously thought.

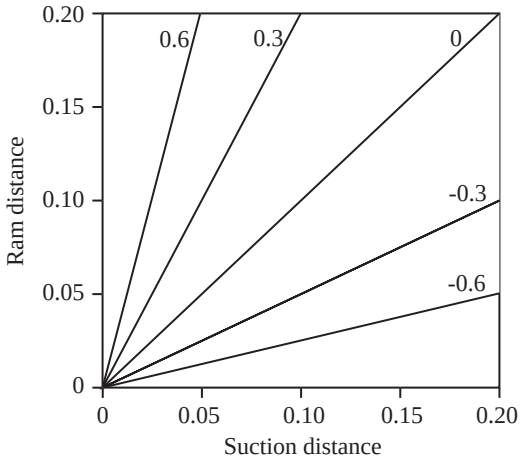

Fig. 10. The relationship between the ram–suction space and the ram–suction index, RSI (Norton and Brainerd, 1993). RSI values are isoclines in this space. Paired values of ram and suction distance along each line give a common value of the RSI. Thus, RSI does not reflect the absolute amounts of ram distance or suction distance, and a given value of the RSI can be formed by any value of ram distance or suction distance paired with the appropriate partner value. These relationships indicate that the RSI will not perform well as a measure of suction- or ram-feeding performance.

Comments on the ram–suction index

In an important contribution intended to provide a benchmark for quantification of the role of ram and suction during prey capture strikes in aquatic vertebrates, Norton and Brainerd (Norton and Brainerd, 1993) proposed the ram–suction index (RSI): (ram distance minus suction distance)/(ram distance plus suction distance). This index ranges from a value of –1, indicating all suction, to a value of 1, indicating a strike that is achieved entirely by ram. Since its introduction, the RSI has been used by a number of authors to characterize prey-capture behavior. It has been used in comparative analyses among species (Gibb, 1997; Ferry-Graham et al., 2001) and in studies within species that focus on topics such as ontogeny (Cook, 1996) and prey type modulation (Lemell and Weisgram, 1997; Nemeth, 1997b; Ferry-Graham, 1998). In the light of the results of this study, we highlight two concerns about the RSI that caution against its use as a measure of ram or suction performance.

First, our finding that suction distance does not differ significantly among species traditionally thought to exemplify model ram and suction feeders indicates that this variable is not a robust measure of the contribution of suction to prey-capture events. The expected exponential decline in flow velocity with distance from the mouth (Muller et al., 1982) suggests that suction distance is unlikely to perform well as a measure of suction-feeding performance. Our finding of little interspecific variation in suction distance suggests the possibility that previous reports of differences among species in the RSI may largely reflect differences in ram distance. Unfortunately, it is difficult to confirm this because ram and suction distance have not been separately reported in studies that use the RSI.

Second, because the RSI is a ratio, it can obscure variation among feeding sequences in the magnitude of ram or suction distance. The RSI is the ratio of the difference between ram and suction and their combined total. A plot of the ram–suction space (Fig. 10) illustrates that RSI values exist as isoclines. Any value of RSI can be formed by any value of ram distance as long as it is combined with the appropriate value of suction distance. Put another way, two feeding sequences with very different values of ram can have the same RSI value, given appropriate suction distances. Thus, RSI values reflect the relative amount of ram and suction distance, but can obscure differences in the absolute amount of these quantities. It is the absolute values of ram and suction distance that we expect to be most important with respect to overall prey-capture performance.

Measuring ram- and suction-feeding performance

A major goal in studies of the functional morphology of feeding in fishes is to identify key elements of feeding performance that can be measured on individual fishes and used in comparative studies that seek to interpret the diversity of form and behavior. Do ram distance and suction distance adequately characterize important aspects of feeding ability in aquatic feeding vertebrates? We conclude that the two measures may, with qualifications, be used to assess certain elements of the prey-capture methods used by fishes, but that neither should be used by itself as a measure of feeding performance.

In this study, differences among species in ram distance reflected differences in feeding ecology. Species that feed largely on highly elusive prey tended to demonstrate larger ram distances. In addition, ram distance generated differences in the approach velocity of the predator, with those same species achieving higher velocities (Fig. 9). However, the relationship between ram distance and attack velocity need not hold. If strike kinematics were particularly slow, a large value of ram distance could be achieved with a slow approach velocity. Combined measures of ram distance and attack velocity appear to be a more promising approach to characterizing this component of the strike.

The prognosis may not be as good for suction distance. We detected no differences among species in this variable (Table 4; Fig. 4), despite the fact that previous studies have found that some of these species generate different maximum values of buccal pressure and that the cichlids used eat very different prey types (Barel, 1983; Van Leeuwen and Muller, 1983; Van Leeuwen and Muller, 1984; Norton and Brainerd, 1993). Our findings may be understood in the light of previous hydrodynamic considerations of the consequences of variation in buccal pressure (Muller et al., 1982). If water velocity declines in proportion to the cube of distance from the mouth (Muller et al., 1982), then a linear relationship between velocity at the mouth opening and suction distance would not be expected. Because of this exponential relationship, large differences in buccal pressure among species, or among strikes by the same fish, will result in relatively small changes in suction distance that may be difficult to measure. Empirical studies are needed that quantify the relationship between buccal pressure, velocity at the mouth opening and suction distance. For example, to our knowledge, there have been no empirical tests with living fish of the predictions of Muller et al. (Muller et al., 1982) that water velocity will decline as an inverse function of d^3. Nevertheless, given the expectation that suction distance will scale as a function of the inverse of d^3, a positive relationship would still be expected. To be useful, suction distance will need to be measured at a fine scale with low error.

Measuring suction distance with low error is further complicated by the fact that this variable is sensitive to differences in the physical properties and behavior of prey. Variation among prey in size, density and shape will influence their susceptibility to the induced flow of the predator, making it difficult to compare the results of studies performed with different experimental prey. In addition, living prey often attempt to escape from the striking predator, resulting in variation among prey and among sequences in the resistance of the prey to the water flow generated by the predator. In the present study, guppies usually performed a fast-start escape response immediately prior to capture. The influence of variation in the behavior and morphology of prey on suction distance is discussed in detail by Norton and Brainerd (Norton and Brainerd, 1993).

An additional difficulty with suction distance is that it may not reflect all of the suction effort of the predator. The actions of suction feeding will pull predators towards their prey just as they draw the prey towards the predator (Van Leeuwen and Muller, 1984). Forward movement of the predator due to suction would be measured as part of ram distance in a study such as ours. In some systems, this effect may be particularly pronounced and may even result in a situation where very little movement of the prey is detected despite considerable suction-powered rostral motion of the predator (Aerts et al., 2000a).

To resolve interspecific differences in the generation of suction, careful measures of suction distance will need to be combined with direct measures of water velocity in front of the mouth and of the volume of water drawn in during prey capture. These measures will almost certainly be strongly size-dependent, and the integration of body size into our understanding of prey-capture diversity is currently lacking. These pieces of information taken together may hold the greatest promise as measures of suction-feeding performance.

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