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Does Feeding Behavior Facilitate Trophic Niche Partitioning in Two Sympatric Sucker Species from the American Southwest?*

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ABSTRACT

We examined two sympatric desert fishes, Sonora suckers (*Catostomus insignis*) and desert suckers (*Pantosteus clarkii*), and asked, does feeding behavior facilitate trophic niche partitioning? To answer this question, we conducted laboratory-based feeding trials to determine whether morphology alone facilitates the diet separation between the relatively unspecialized, omnivorous Sonora sucker and the more morphologically specialized, algivorous desert sucker or whether behavioral differences accompany morphological specialization. We predicted that (1) algivorous desert suckers would maximize contact between jaws and substrate and produce a large mouth-gape to facilitate scraping attached food-material; (2) omnivorous Sonora suckers would be more effective suction feeders when consuming unattached food items from the benthos; and (3) because they are anatomically specialized for scraping, desert suckers could not alter their feeding behavior when presented with different prey types, whereas relatively unspecialized Sonora suckers could vary behavior with prey type. We found that both species maximized jaw contact when feeding on benthic-attached food, although desert suckers produced a greater gape area. We also found that Sonora suckers were more effective suction feeders when feeding on benthic-unattached prey. Counter to our initial predictions, both species altered key aspects of feeding behavior in response to different prey types/locations. It appears that both sucker species can function as generalist feeders to exploit a variety of prey types within their natural habitat; indeed, this behavioral versatility may allow desert and Sonora suckers to respond to the cyclic en-

vironmental changes that are characteristic of the aquatic habitats of the American Southwest.

Introduction

Niche differentiation allows two sympatric species to partition resources within a habitat and avoid competition—thus enabling the two species to coexist (e.g., Werner 1977). In fishes, specialized feeding morphology and behaviors may facilitate enhanced performance on particular prey types and allow closely related species that focus on different prey types to co-occur through trophic partitioning (Liem 1978; Nemeth 1997; Hulsey and García de León 2005). However, morphological specializations could also become a liability in times of environmental change: a species specialized for a particular prey type is likely to suffer if that prey type is lost (Olden et al. 2008). Thus, the ability to alter behavior via modulation—where output from the central nervous system changes how muscles are activated and bones are displaced—may enable individuals of a given species to survive by allowing them to consume a variety of prey types (Liem 1980).

However, if an organism specializes on one feeding mode, there may be intrinsic costs to capture performance in other modes. For example, suction- and biting-based feeding behaviors clearly place competing demands on prey capture anatomy and behavior: oral jaw velocity, shape of the oral opening, oral jaw force, and muscle activation patterns are consistently different when these two behaviors are compared between and even within a single species (Wainwright and Richard 1995; Alfaro et al. 2001; Westneat 2004). Fishes that are trophic generalists and capture different types of prey using a nonspecialized morphology modulate their prey capture movements (Sanderson 1991; Nemeth 1997; Van Wassenbergh et al. 2006); modulation alters (modifies) cranial movements to produce a suite of behaviors that are tailored to different prey types. However, because functional trade-offs are thought to increase with increasing morphological specialization (Bouton et al. 1998), anatomically specialized fishes are predicted to be inferior to more generalized fishes when feeding on “new” or unusual prey types (Van Wassenbergh et al. 2006), although the impact of such hypothesized trade-offs on performance is seldom documented (but see Sanderson 1991; Ferry et al. 2012).

Two genera of catostomid suckers, *Catostomus* and *Pantosteus*, employ specialized jaw morphologies for procuring food from the benthos. These genera are currently listed as confamilial genera (Nelson 2006), although recent work suggests the two lineages merit subfamily status (Unmack et al. 2010). Representatives of

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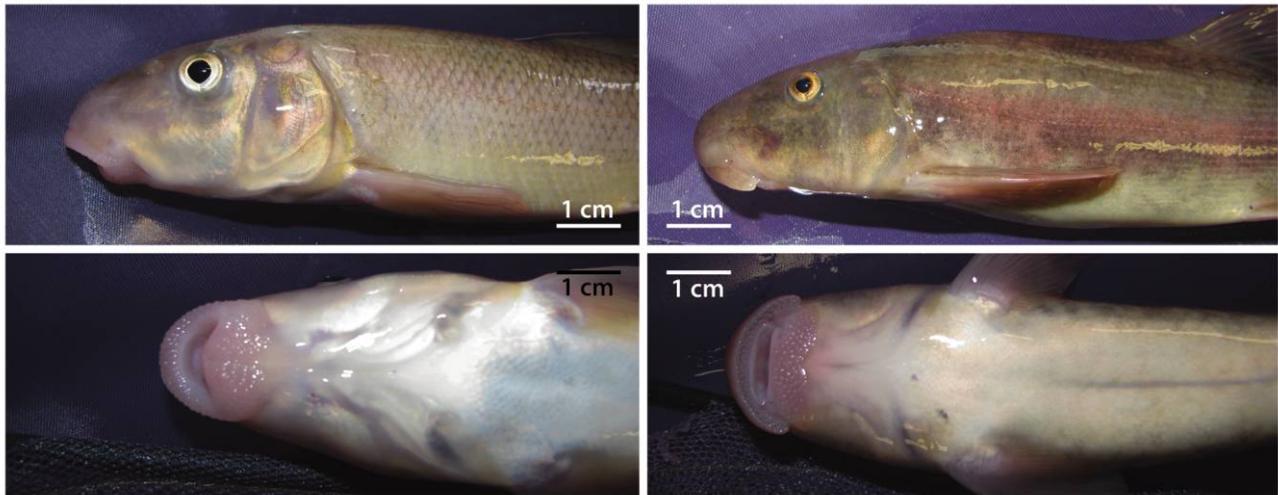


Figure 1. The desert sucker (*right*) has a broader mouth relative to the thinner, narrower mouth of the Sonora sucker (*left*). We used a Canon S5IS digital camera to capture images of lateral (*top*) and ventral (*lower*) views of one euthanized individual of each species. Images were cropped to isolate the area of interest, but brightness, contrast, and sharpness were not modified.

each lineage are distributed across much of North America and often co-occur with high population numbers of both species present in a given creek or river (Minckley and Marsh 2009). In central and northern Arizona and New Mexico, *Catostomus insignis* and *Pantosteus clarkii* are endemic representatives of these two genera that possess two distinct feeding morphologies (Clarkson and Minckley 1988); unfortunately, populations of these two sucker species appear to be in decline due to negative impacts of anthropogenic habitat modification (AZGFD 2002; Minckley and Marsh 2009). Although these two species are superficially anatomically similar, the ability to co-occur in a habitat suggests an ecological mechanism that reduces competition, and subtle variation in the jaw morphology (fig. 1) across the two lineages may provide that mechanism.

Following the ecomorphological paradigm (Wainwright and Reilly 1994), we expect that distinct feeding morphologies have evolved to enhance different feeding strategies. A morphological study by Clarkson and Minckley (1988) determined that desert suckers, relative to Sonora suckers, have a longer and wider mouth, larger lower lips, and a wider but less deep head. The Sonora sucker (*Catostomus insignis*), considered a generalist benthic omnivore, has a relatively small gape that may enhance suction production (Wainwright et al. 2007) when these fish capture small invertebrates. The wider mouth and cartilaginous plate of the desert sucker, often considered an algae specialist (*Pantosteus clarkii*), may facilitate the removal of algae from the substrate (fig. 1; Clarkson and Minckley 1988). Gut-content studies support this hypothesized diet partitioning: Sonora suckers consume more invertebrate prey than desert suckers, both in terms of gut content volume (58% vs. 14%, respectively) and frequency of occurrence in guts (97% vs. 70%), whereas desert suckers consume more filamentous algae and diatoms than Sonora suckers by both volume (10% vs. 1.5%, respectively) and

frequency (72% vs. 40%; Clarkson and Minckley 1988). Stable isotope analyses also indicate a higher proportion of animal tissue in the diet of Sonora suckers relative to desert suckers (Marks et al. 2010; Pilger et al. 2010), which provides further support for the hypothesis of trophic niche partitioning.

Differences in morphology may provide the fundamental mechanism that underlies niche partitioning between these two species. For example, the “scraping plate” of the lower jaw and the wide mouth-gape of the desert sucker may enhance its ability to acquire attached algae and associated interstitial invertebrates. However, that same morphology could become a liability when a desert sucker attempts to consume individual prey items by drawing them into the mouth via suction, because a smaller anatomical gape is optimal under those circumstances (Skorczewski et al. 2012).

In addition, although anatomical specialization may enable a given species improved performance on a particular prey type, accompanying behavioral differences may enhance morphological traits, thus allowing a species improved performance on its primary food item. For example, the Sonora sucker (Minckley and Marsh 2009) has a smaller gape that may enhance suction-feeding performance (Wainwright et al. 2007). Sonora suckers could also enhance suction production by producing a very large degree of cranial rotation—which is associated with suction feeding in other fish species (Gibb and Ferry-Graham 2005; Westneat 2005). Similarly, because suction feeding is most effective when applied against a substrate (Nauwelaerts et al. 2007), Sonora sucker individuals could focus their foraging efforts entirely on benthic prey items.

It is also possible that by altering cranial movements in response to a new prey or unusual type, a fish can overcome any potential handicap imposed by morphology. In this scenario, when feeding on individual, unattached prey items, desert suckers

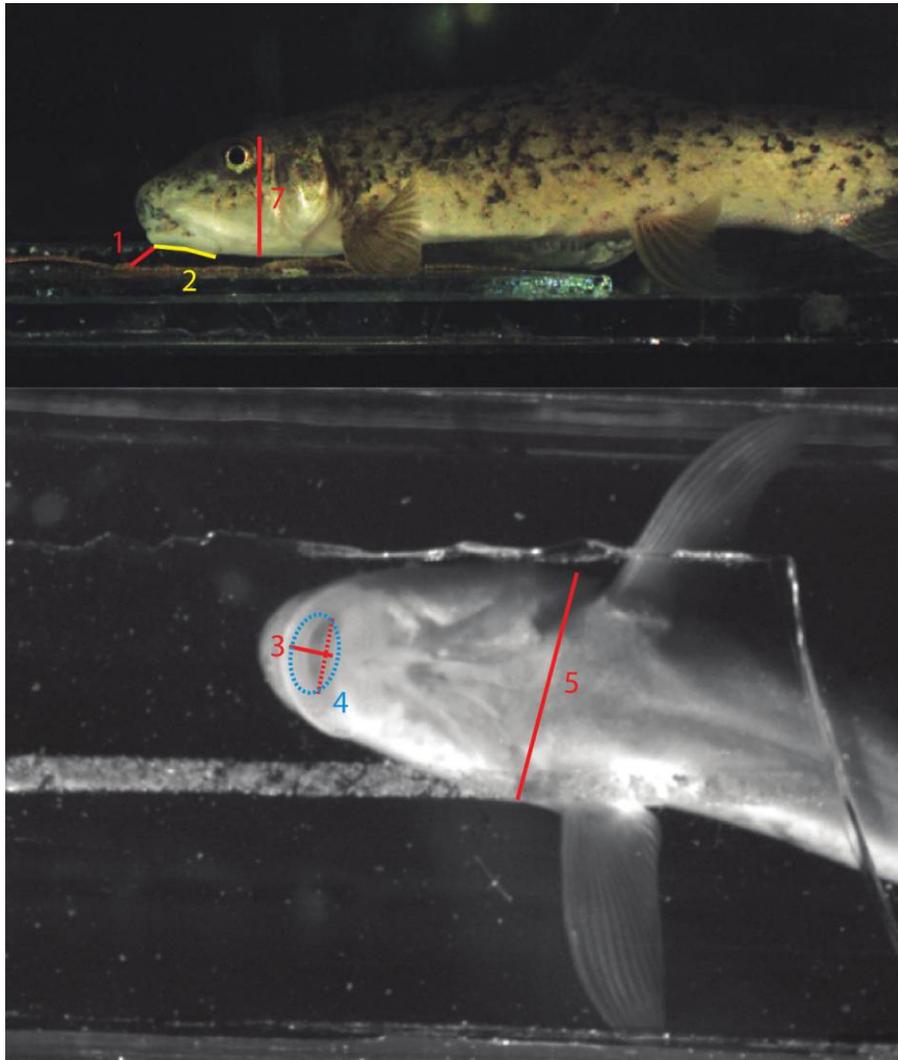


Figure 2. Prey capture behavior was recorded synchronously from a dorsal and ventral view to allow the measurement of a suite of kinematic variables. The following variables were measured as indicated by colored lines/symbols on each panel: (1) prey displacement; (2) gape angle (yellow line); (3) gape (gape height); (4) gape area (blue circle); (5) cranial expansion; (7) hyoid depression. The red dotted line (transverse to the mouth) was used to assess gape ratio (a proxy for the circularity of the mouth) and gape area.

could “choose” to produce a smaller gape and greater cranial rotation, as an increase in the magnitude of these two traits is associated with increased suction performance (Gibb and Ferry-Graham 2005; Wainwright et al. 2007; Skorzewski et al. 2012). In this manner, modulation (Liem 1980; Nemeth 1997; Oufiero et al. 2012) of prey-capture behavior could compensate for the potential handicaps imposed by a specialized feeding apparatus.

Is it morphological specialization that facilitates the putative trophic separation between Sonora and desert suckers in the rivers of the desert Southwest, or are there behavioral differences that accompany morphological specialization? Based on ecological and morphological characteristics of these two species, we seek to identify behavioral differences between the two species in response to different prey types presented in different locations by considering three functional hypotheses. (1) We hypothesize

that desert suckers are scraping specialists that will seek to maximize contact between their jaws and the substrate to facilitate removing attached prey items. Based on this, we predict that, relative to Sonora suckers, desert suckers produce a larger mouth gape, gape area, and gape angle (approaching 180° , which would represent full contact of the upper and lower jaws with the substrate) when feeding on benthic-attached prey. (2) We hypothesize that Sonora suckers are more generalized omnivores (relative to desert suckers) and will produce greater suction pressure when feeding on unattached prey items. Based on this, we predict that Sonora suckers use their smaller-diameter mouths to produce a flow field that will displace unattached prey over a greater distance (relative to the larger-mouthed desert suckers) when consuming unattached, benthic prey (Wainwright et al. 2007). Further, we expect that Sonora suckers will produce a smaller,

Table 1: Variable loadings for components 1 and 2 as generated by principal components analysis when six kinematic variables were considered for desert and Sonora suckers

Variable	Component	
	1	2
Gape area	-.876*	-.126
Gape ratio	.741*	.544
Hyoid depression	.862*	-.080
Head expansion	.714*	-.243
Time to maximum hyoid depression	.031	.915*
Time to maximum head expansion	-.329	.910*

Note. Variables that loaded heavily for a given factor (greater than 0.6 or less than -0.6) are indicated with an asterisk. Principal component (PC) factor 1 is heavily weighted by the variable associated with magnitude of mouth opening (gape) and degree of cranial expansion; PC factor 2 is heavily weighted by the timing of cranial expansion during feeding.

more rounded gape, and greater buccal expansion when capturing unattached prey, because these behavioral traits should enhance suction-feeding performance (Gibb and Ferry-Graham 2005; Wainwright et al. 2007; Skorczewski et al. 2012). (3) We hypothesize that desert suckers employ an invariant feeding behavior to capture a variety of prey types, while Sonora suckers have a repertoire of behaviors that they employ to obtain a variety of prey types. The specialized morphology of desert suckers may limit their behavioral repertoire to only allow benthic scraping (Clarkson and Minckley 1988; Sanderson 1991; Ferry et al. 2012), while Sonora suckers are more likely to consume a variety of prey types in the wild (Clarkson and Minckley 1988). Thus, we predict that Sonora suckers generate a distinct suite of cranial movements when feeding in the water column versus when feeding on unattached prey located on the bottom. Because they are anticipated to modify their behaviors to accommodate the physical requirements of different feeding locations, we expect that Sonora suckers will produce a smaller gape, greater buccal expansion, and more rapid movements when feeding in the water column, relative to feeding from the substrate. In contrast, desert suckers are not expected to alter their feeding behavior between locations because a stereotyped or unvarying suite of movements may be most effective for removing attached materials from the substrate.

Material and Methods

Sonora suckers and desert suckers were captured with hoop nets or by electrofishing from Fossil Creek, Arizona, a small desert stream in the Verde River watershed of the southwestern United States where both species naturally co-occur; all fish collected were between 100 and 120 mm standard length. After capture, fish were moved to 38-L aquaria and acclimated to lab conditions for at least 2 wk. During the acclimation period, fish were maintained on commercial flake food (TetraMin Tropical Flakes, TetraMin) and frozen "bloodworms" (chironomid larvae, Sally's Bloodworms, San Francisco Bay Brand). After

feeding trials were complete, fish were euthanized with an overdose of tricaine methanesulfonate and then preserved. All animal care and research procedures were conducted under Northern Arizona University's Institutional Animal Care and Use Committee protocol 07-014.

During the feeding trials, fish were placed in a custom-built tank that allowed us to capture simultaneous and unobstructed lateral and ventral views of feeding events. We used two Phantom v5.1 cameras (Vision Research) and recorded digital images at 700 frames per second. Both sucker species were recorded feeding on three prey types, which were selected to represent food items that these fish often encounter in the wild: benthic-attached prey (ground commercial fish-food glued in a thin film onto a glass plate), benthic, nonelusive prey (i.e., dead chironomid larvae), and midwater nonelusive prey (frozen brine shrimp). Lateral and ventral views of three feeding events were recorded for each individual (3 individuals per species) for each prey type (thus, nine feeding events were recorded for each individual). Eight points from ventral images and 17 points from lateral images were tracked using anatomical landmarks on the head and body of each fish with the image analysis program DIDGE (developed by Alistair Cullum of Creighton University). In this manner, we quantified characteristics of

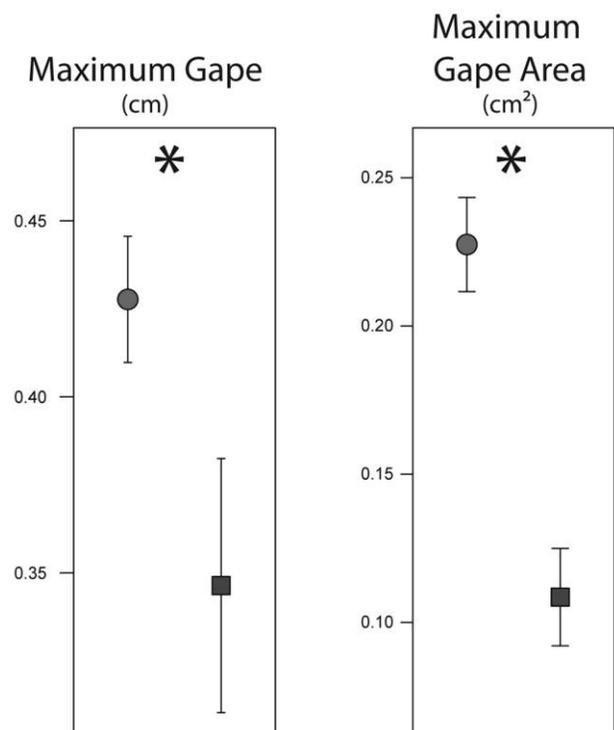


Figure 3. Desert suckers (circles) and Sonora suckers (squares) produce a similar gape (as measured by gape height) when scraping attached food material from the substrate (benthic-attached prey type). However, desert suckers have wider mouths and produce a greater gape area; see hypothesis 1 ("Introduction"). Variables are given here as mean values \pm 1 SEM; an asterisk indicates a significant difference as analyzed with a one-tailed Student's *t*-test.

Table 2: Means of displacement variables (± 1 SEM) as quantified from high-speed digital video sequences of desert and Sonora suckers consuming three prey types placed in different locations

Prey type	Maximum gape (cm)	Gape area (cm ²)	Gape ratio (roundness, cm/cm)	Prey displacement (cm)	Maximum hyoid depression (%)	Maximum head expansion (%)	Maximum gape angle
Desert sucker:							
Benthic attached	.428 \pm .018	.227 \pm .016	.638 \pm .049	.000 \pm .000	1.082 \pm .432	7.919 \pm 1.341	180.0 \pm .0
Benthic unattached	.409 \pm .040	.229 \pm .016	.582 \pm .089	.180 \pm .011	2.084 \pm .561	10.136 \pm 2.024	180.0 \pm .0
Midwater	.366 \pm .033	.181 \pm .013	.603 \pm .116	.381 \pm .044	3.822 \pm .724	20.279 \pm .638	180.0 \pm .0
Sonora sucker:							
Benthic attached	.346 \pm .036	.109 \pm .016	.891 \pm .076	.000 \pm .000	2.961 \pm .735	12.774 \pm 1.992	180.0 \pm .0
Benthic unattached	.343 \pm .030	.114 \pm .008	.910 \pm .038	.401 \pm .078	6.425 \pm 1.154	18.065 \pm 3.596	150.7 \pm 8.3
Midwater	.339 \pm .020	.096 \pm .012	.914 \pm .043	.386 \pm .036	6.078 \pm .471	18.420 \pm 1.505	149.4 \pm 2.5

food-capture behavior using nine kinematic variables (fig. 2): (1) prey displacement, or how far the food item moved when captured by a fish; (2) maximum gape angle, or the largest angle formed by the upper and lower jaws during food capture; (3) maximum gape, or the maximum distance between the upper and lower jaws during the feeding event; (4) maximum gape area, or the area formed by measuring the sagittal and transverse dimensions of the gape and modeling the gape as an ellipse (fig. 2); (5) maximum lateral cranial expansion, or the largest change in the distance between the outer edge of the opercula during the feeding event expressed as percent increase (i.e., $[\text{max width} - \text{resting width}] \times \text{resting width}^{-1} \times 100$); (6) time to maximum cranial expansion or the elapsed time from beginning of mouth movement to maximum cranial expansion; (7) maximum hyoid depression, or the change in head depth, measured beneath the eye and expressed as percent increase ($[\text{max depth} - \text{resting depth}] \times \text{resting depth}^{-1} \times 100$); (8) time to maximum hyoid depression or elapsed time from the onset of mouth movement to maximum hyoid depression; and (9) gape ratio, which is calculated as gape length divided by gape width, a measure of gape aspect ratio (where a perfectly square or round gape would have a gape ratio of 1). From all trials for a given prey type with a given individual, we calculated the arithmetic mean of each kinematic variable

for use in statistical analyses. Log transformations were employed on individual variables (as needed) to ensure normality and homogeneity of variance.

One-tailed *t*-tests ($P = 0.1$) considering potential effects of species were used to test specific functional predictions based on hypotheses 1 and 2, as outlined in "Introduction." Tests were one-tailed to reflect the directionality of our predictions (hypotheses 1 and 2). To address the question of potential variation in prey capture behavior within a species and among prey types (hypothesis 3), we examined six kinematic variables that play a key role in suction production during food capture (Gibb and Ferry-Graham 2005, Westneat 2005): maximum gape area, gape ratio (height:width), maximum hyoid depression, time to maximum hyoid depression, maximum cranial expansion, and time to maximum cranial expansion (fig. 2). We used principal components analysis (PCA) to consolidate six potentially correlated kinematic variables into compound variables. For this PCA we employed a correlation matrix and retained factors with an eigenvalue greater than 1, which generated two compound variables. To test hypothesis 3, the compound variables generated by the PCA were used as dependent variables in two repeated-measures (because each fish individual was measured multiple times feeding on each prey type), two-way analyses of variance. For this model, we

Table 3: Means of timing variables (± 1 SEM) as quantified from high-speed digital video sequences of desert and Sonora suckers consuming three prey types placed in different locations

Prey type	Time to maximum hyoid depression	Time to maximum head expansion
Desert sucker:		
Benthic attached	66.2 \pm 11.2	108.5 \pm 14.0
Benthic unattached	41.7 \pm 1.4	85.4 \pm 1.1
Midwater	52.2 \pm 12.4	55.7 \pm 15.9
Sonora sucker:		
Benthic attached	69.1 \pm 14.1	102.4 \pm 24.0
Benthic unattached	61.4 \pm 14.6	76.2 \pm 8.5
Midwater	43.0 \pm 11.7	57.3 \pm 13.3

considered potential “species” and “prey-type” effects and “species \times prey-type” interactions in a one-tailed test. After examining the loadings of the PC factors, we were able to generate specific predictions about the ANOVA that also allowed one-tailed hypothesis testing ($P < 0.10$). When considering the compound variables generated by the PCA (table 1) using ANOVA, Sonora sucker were hypothesized to have higher-amplitude variable displacements (which loaded on PC 1) and more rapid movements (as measured by variable timings, which loaded on PC 2) for all cranial variables except gape (which is expected to have a smaller amplitude). In addition, our expectations for potential prey type effects also yielded a one-tailed prediction: feeding events on benthic-attached food were hypothesized to be lower amplitude (PC 1) and slower (PC 2), relative to feeding events on unattached food items. All statistical analyses outlined here were performed in SPSS, version 21.0 (IBM, Armonk, NY).

Results

Individuals of both sucker species required extensive acclimation to lab conditions before they were willing to feed under the camera lights. In particular, desert suckers were reluctant to feed when offered midwater prey and often waited until the prey settled onto the substrate. During all feeding events in both sucker species, we observed a suite of unusual features of prey capture. First, both species produced little or no cranial elevation or hyoid depression. This was somewhat surprising because these movements are often thought to contribute to the buccal-cavity expansion that is required for suction production in many teleosts (Gibb and Ferry-Graham 2005). The small gape of Sonora suckers, in particular, is expected to enhance suction production, so the lack of cranial elevation and hyoid depression for this species was unanticipated. Another unusual feature of feeding behavior for both sucker species was that lower jaw rotation (or depression) was obscured by a co-occurring movement of the lower, fleshy “lip,” which moves anteriorly at the same time that the upper jaw protrudes anteriorly.

Benthic-Attached Prey

We predicted that, relative to Sonora suckers, desert suckers would produce greater contact between their jaws and the substrate when feeding on benthic-attached food items (hypothesis 1). Somewhat surprisingly, gape angle did not differ between the two species: all individuals of both species consistently opened their jaws to 180° to place them flush against the substrate. However, when feeding on attached, benthic food items, the maximum gape area ($t = 5.21$, $df = 4.0$, $P = 0.003$) and maximum gape, or gape height ($t = 2.02$, $df = 2.93$, $P = 0.07$), were significantly larger in desert suckers (tables 2, 3). During trials on benthic-attached food items, Sonora sucker individuals produced a gape that was $0.35 (\pm 0.04)$ cm with a gape area of $0.11 (\pm 0.02)$ cm², whereas desert suckers produced $0.43 (\pm 0.02)$ cm and $0.23 (\pm 0.02)$ cm², respectively (fig. 3).

Benthic-Unattached Prey

We expected that, relative to desert suckers, Sonora suckers would displace unattached food items over a greater distance and produce a smaller, more rounded gape and greater cranial and buccal expansion when capturing unattached food items from the substrate (hypothesis 2). This hypothesis was supported: when feeding from the benthos, Sonora suckers displaced food items ~ 1 mm farther than desert suckers ($t = 2.81$, $df = 2.1$, $P = 0.051$). Sonora suckers also formed a nearly circular mouth opening (gape ratio ≈ 1) that was significantly different ($t = 3.40$, $df = 2$, $P = 0.025$) from the mouth opening ratio of desert suckers (gape ratio ≈ 0.34 ; fig. 4). Gape area also differed between species ($t = 6.47$, $df = 3.1$, $P = 0.004$; see tables 2, 3), though maximum gape ($t = 1.31$, $df = 3.7$, $P = 0.266$) did not: Sonora suckers produced a gape that was $0.34 (\pm 0.03)$ cm with a gape area of $0.11 (\pm 0.01)$ cm², whereas desert suckers produced gape heights and areas of $0.41 (\pm 0.04)$ cm and $0.23 (\pm 0.02)$ cm², respectively.

Cranial Expansion

Two key components of buccal expansion in most teleost fishes are cranial rotation and hyoid depression. Cranial rotation for both of sucker species considered here was either not present or so small as to be masked by measurement error (M. W. O'Neill, personal observation). Hyoid depression was also quite small, but was significantly larger in Sonora suckers ($6.4\% \pm 1.2\%$) than in desert suckers ($2.1\% \pm 0.6\%$; $t = 3.38$, $df = 2.9$, $P = 0.023$). In addition, Sonora suckers tended to take longer to reach maximum hyoid depression (61.4 ± 14.6 ms), relative to desert suckers (41.7 ± 1.4 ms), although this difference was not significant ($t = 1.34$, $df = 2.0$, $P = 0.155$). Sonora suckers expanded the opercula laterally to a greater extent ($t = 1.92$, $df = 3.2$, $P = 0.073$) and more quickly ($t = 1.08$, $df = 2.1$, $P = 0.196$; fig. 5), thereby producing a more rapid movement (-10 ms) and greater expansion ($+8.8\%$), relative to desert suckers. Though expansion velocity did not differ significantly between species, the increased velocity in combination with significantly increased expansion distance should allow Sonora suckers to produce a greater negative buccal pressure, relative to desert suckers.

Behavioral Modulation

We initially hypothesized that desert suckers would employ a single, invariant feeding behavior to capture all prey types, while Sonora suckers would produce distinct behaviors to obtain different types of prey from the environment (hypothesis 3). Principal components analysis of six kinematic variables resulted in two factors that together summarized approximately 79% of total variance (table 1). Displacement variables associated with mouth opening and cranial and buccal expansion (maximum gape area, gape ratio, maximum hyoid depression, maximum cranial expansion) loaded on PC factor 1, whereas timing variables related to head expansion (time to maximum hyoid

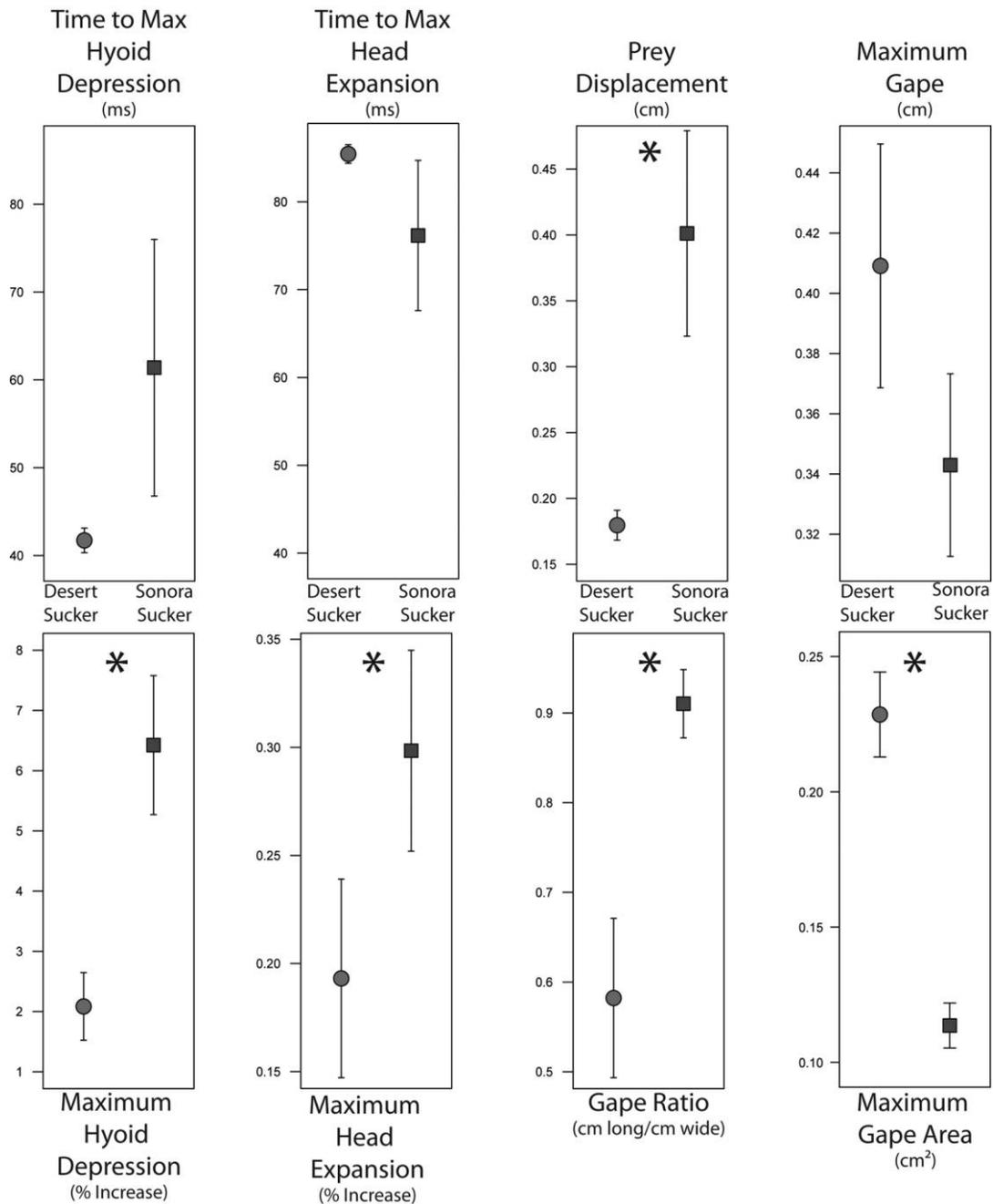


Figure 4. When feeding on unattached, benthic prey-items, the cranial movements of Sonora suckers (squares) are modulated in a manner that is likely to improve suction performance; see hypothesis 2 (“Benthic-Unattached Prey”). Relative to desert suckers (circles), Sonora suckers (squares) consistently produce a smaller, more rounded gape; expand the cranial cavities to a greater extent; and suck prey in from a greater distance away. Variables are given as mean values \pm 1 SEM; an asterisk indicates a significant difference as analyzed with a Student’s *t*-test. A color version of this figure is available online.

depression, time to maximum cranial expansion) loaded on PC factor 2. In the two-way, one-tailed, repeated-measures ANOVA for PC factor 1, the “prey type \times species” interaction term was significant, indicating that the two species respond differently to different food types (fig. 6; table 4). The primary difference between the two species appears to be the response

to benthic-unattached prey items. PC factor 1 suggests that Sonora suckers use larger buccal and cranial expansion (greater hyoid depression and cranial expansion) and a smaller, more round gape when feeding on benthic-unattached prey, relative to benthic-attached prey. For Sonora suckers, movements during capture of benthic-unattached prey were similar to move-

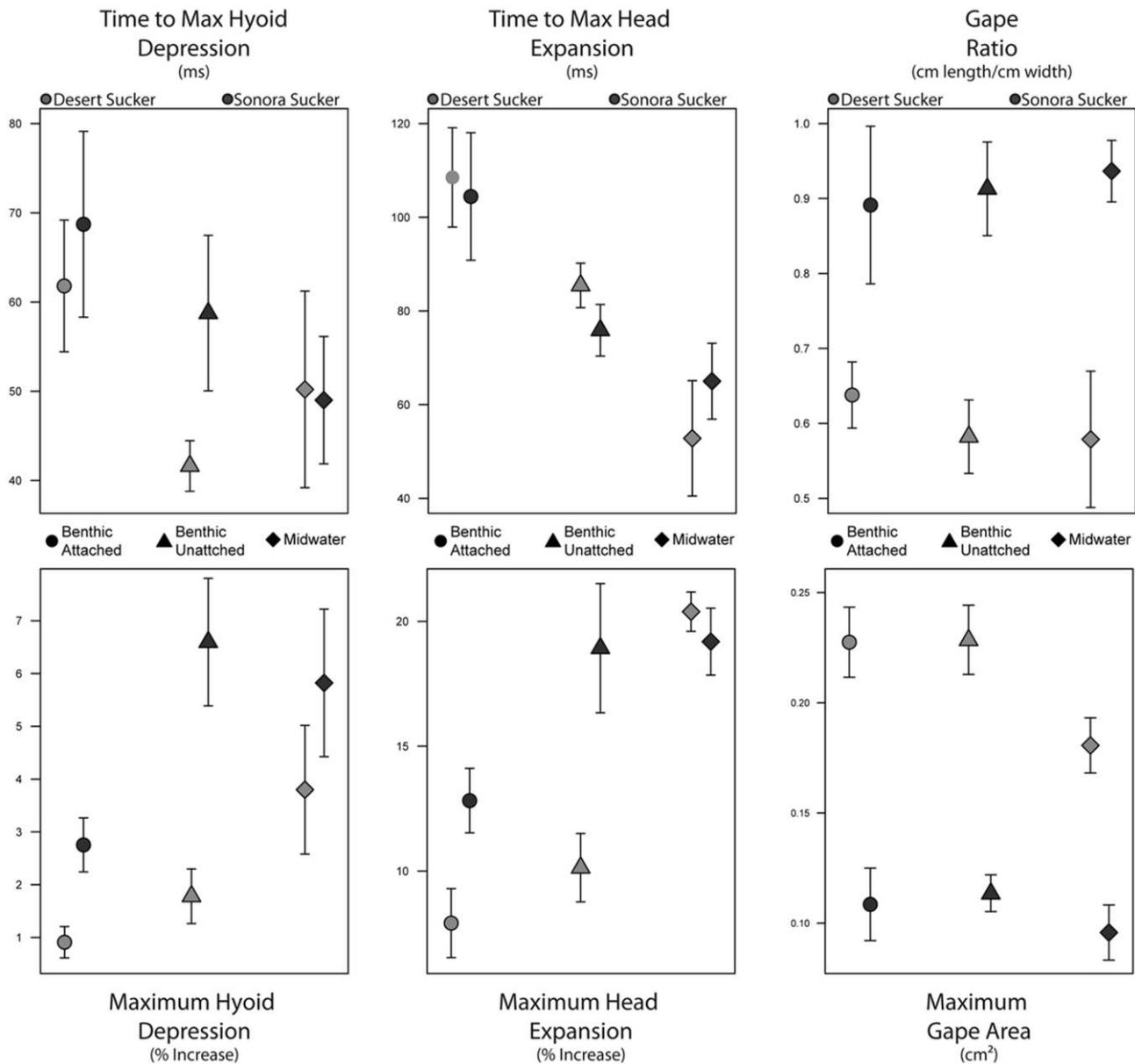


Figure 5. Sonora suckers (black) and desert suckers (gray) modulate aspects of feeding behavior depending on food type and location; see hypothesis 3. Mouth opening (as quantified by gape and gape ratio) is relatively invariant across prey types; however, both species alter other parameters that may improve suction production. Circles represent benthic-attached prey, triangles represent benthic-unattached prey, and diamonds represent midwater prey. Variables are given as mean values \pm 1 SEM; see text for an explanation of significant differences. A color version of this figure is available online.

ments during midwater prey capture events. For desert suckers, the movements produced when feeding on benthic-unattached food items were similar to the movements produced when feeding on benthic-attached food. Because the one-tailed, two-way, repeated-measures ANOVA revealed that there was no prey type \times species interaction for PC factor 2 (table 4), the interaction term was removed from the model (Sokal and Rohlf 1995). After the interaction term was removed, the nested ANOVA model was rerun to consider only potential effects of species and prey type. In the modified model, there was no

significant effect of species, but there was an effect of prey type ($P = 0.06$). This finding suggests that both species altered the timing of feeding movements by expanding their buccal and cranial cavities more rapidly when feeding on benthic-unattached and midwater food items.

Midwater Prey

Finally, we performed a one-tailed t -test on the variable "prey movement" for midwater food items. This analysis revealed

Table 4: Two-way, repeated-measures ANOVAs consider potential effects of species, prey type, and species \times prey type interactions for two compound variables that were derived from principal component analysis (PCA factor 1 and PCA factor 2)

	Sum of squares	df	Mean square	<i>F</i>	Significance
PCA factor 1:					
Within-subjects main effect (prey type)	4.045	2	2.023	23.022	<.001
Between-subjects main effect (species)	10.846	1	10.846	82.916	.001
Between-subjects interaction effect	.883	2	.441	5.024	.039
PCA factor 2:					
Within-subjects main effect (prey type)	5.928	2	2.964	4.025	.062
Between-subjects main effect (species)	.868	1	.868	.826	.415
Between-subjects interaction effect	.106	2	.053	.072	.931

that there was no difference in the distance that desert and Sonora suckers were able to move food when suction feeding from the water column ($t = 0.09$, $df = 3.86$, $P = 0.467$; fig. 7). Both species were able to move the prey approximately 0.38 cm through the water column and into the mouth.

Discussion

Both Sonora and desert suckers are clearly adapted for benthic feeding. In both sucker species, the anterior jaws appear to be constrained to project down, below the head—even when fish are feeding on free-floating prey in the water column. In addition, the lip apparatus of both of these species (and of other catostomid species) is covered with tactile and chemosensory structures that help these fishes locate cryptic prey attached to or under stones or hidden in accumulated detritus (Miller and Evans 1965). Indeed, the fleshy lower lips of both sucker species appeared to move forward in advance of the lower jaw during lower jaw depression (M. W. O'Neill, personal observation), which indicates active lip movements. We note that such active movements indicate the presence of a heretofore unrecognized muscular mechanism for controlling the lip independently of the jaw. We suggest that sucker lips are used as a prey-detecting tool in a manner similar to the barbels of benthic-feeding lorocariid catfishes (Geerinx et al. 2007).

Because hyoid depression and cranial rotation serve to rapidly enlarge the buccal cavity for suction production, the limited cranial rotation produced by both sucker species was unexpected. However, reduced hyoid depression and cranial rotation are also seen in other benthic-feeding fishes, and may represent an adaptation for substrate feeding. Hyoid depression may be limited by physical interaction with the substrate during prey capture, and cranial rotation could potentially pull the fish jaws away from ventrally located prey (Van Wassenbergh et al. 2009). In fact, benthic-feeding catfish also show reduced cranial rotation and hyoid depression in concert with increased lateral expansion of the buccal cavity (Van Wassenbergh et al. 2009).

Based on the ecomorphological paradigm (Wainwright and Reilly 1994), we initially hypothesized that these two sucker species would be fundamentally different from one another in both feeding morphology and food-capture behavior. We predicted that the more extreme jaw modifications of the desert

sucker would enhance feeding performance on attached food items but would constrain feeding performance on other prey types. Thus, we expected that desert suckers would use a larger gape and greater gape angle to optimize scraping prey from the substrate and that they would be unable to alter this behavior when presented with other prey types in other locations. Somewhat counterintuitively, both sucker species produced $\sim 180^\circ$ gape to press their jaw tips flush against the substrate, which likely improves their ability to scrape prey from substrate by generating maximum jaw-substrate contact. However, the larger gape area and highly modified lower jaw of the desert sucker should make it a superior scraper; we predict that desert suckers feeding in the wild can dislodge a greater volume of attached algae (and associated invertebrates) for a given bite, relative to Sonora suckers.

In contrast, the broader diet and more generalized morphology of the Sonora sucker yielded an a priori expectation that this species would suction feed more effectively from the benthos and could modulate its cranial movements when procuring food items from the water column. In fact, the small, round gape and greater buccal cavity expansion do appear to make Sonora suckers superior suction feeders, at least when feeding on unattached, nonelusive, benthic prey. It is likely that Sonora suckers are better able to procure individual, unattached prey items located on the bottom of a stream or river (particularly macroscopic aquatic invertebrates), relative to desert suckers.

We initially predicted that Sonora suckers would modulate their feeding behavior when consuming different prey types, while desert suckers would be locked into a single behavior type because of their morphological specialization. Sonora suckers do alter both the timing and displacement of key kinematic variables associated with feeding behavior when capturing unattached prey, relative to when scraping from the substrate. This suggests that Sonora suckers are indeed changing behavior in an attempt to optimize suction production against the substrate, where suction feeding is most effective (Nauwelaerts et al. 2007). However, desert suckers also modulate kinematics of capture behavior in an apparent effort to increase suction production, at least when feeding on prey in the water column. Changes in cranial movements that enhance midwater

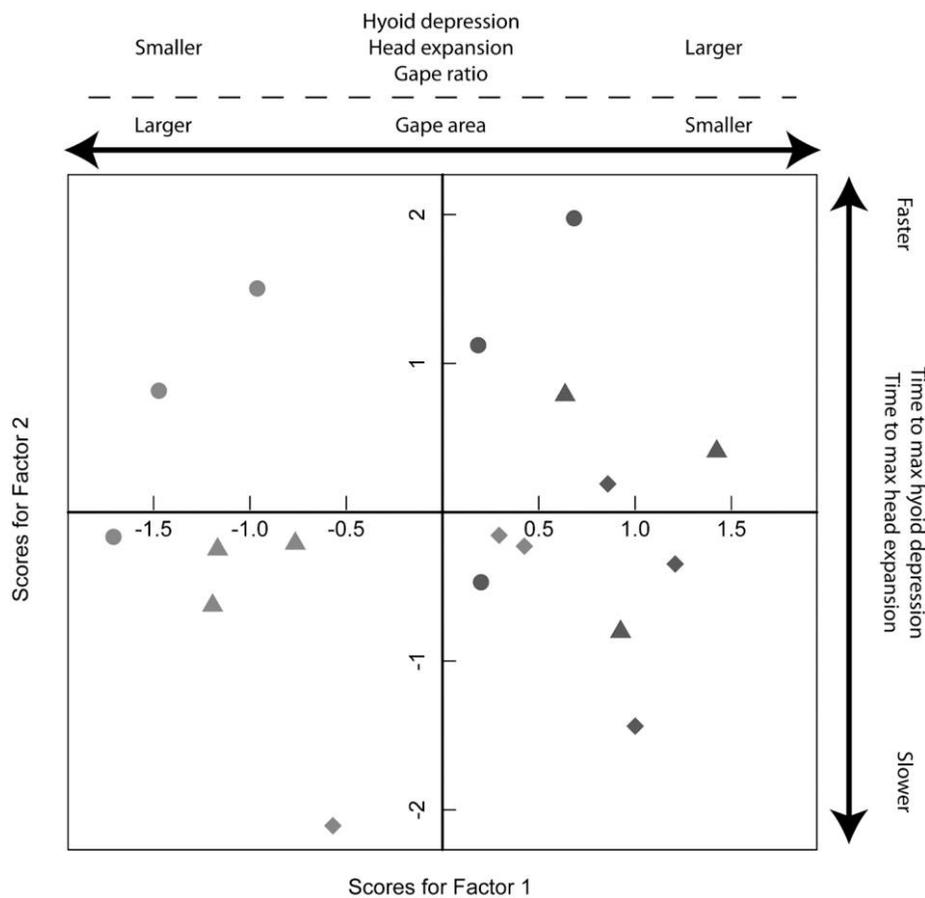


Figure 6. Two principal factors largely distinguish prey capture behavior events by species and prey location in Sonora and desert suckers. Principal component (PC) factor 1 and PC factor 2 summarize six kinematic variables that quantify the feeding behavior of desert and Sonora suckers. Each point represents the PC scores (PC 1 vs. PC 2) for a given individual of a single sucker species when feeding on a particular prey type. Desert suckers are given in light gray, Sonora suckers are given in dark gray, circles represent benthic-attached prey, triangles represent benthic-unattached prey, and diamonds represent unattached midwater prey. A color version of this figure is available online.

feeding are so effective that desert suckers are actually able to draw midwater prey into the mouth from the same distance away from the head as Sonora suckers, in spite of their larger, oblong gape. Thus, despite a very specialized scraping morphology, desert sucker individuals join other trophic specialists such as clariid catfishes and many members of the Cichlidae that modulate feeding behavior to overcome their anatomical specialization when consuming unusual prey types (Wainwright et al. 2001; Van Wassenbergh et al. 2007, 2009; Binning et al. 2009). This finding implies that desert suckers might, like Sonora suckers, function as generalist feeders within their habitat to exploit a variety of prey types.

Because desert suckers may sometimes behave as generalist omnivores, competition between the putative “scraping” and “suction-feeding” suckers may be greater than previously thought. While the scraping morphology of the desert sucker can be employed to consume algae in high-flow areas of streams and rivers where Sonora suckers rarely venture (Clarkson and Minckley 1988), these fish might compete on a daily basis with Sonora suckers for invertebrate prey items. In this scenario,

suckers are similar to African rift lake cichlids, which are known to have specialized feeding morphologies but generalist diets (often termed “Liem’s paradox”; Liem 1980). However, it is also possible that algae (and associated invertebrates) are the typical prey of desert suckers and are procured via their specialized scraping morphology and behavior. In this scenario, instead of the specialized morphology acting as a refuge against prey scarcity, desert suckers use their specialized morphology on a daily basis, and the ability to modulate head and jaw movements allows these fish to become omnivores as a behavioral refuge. When placed in a broader context, these results suggest that desert suckers can behaviorally overcome potential morphological handicaps to effectively capture a variety of prey. This may allow these fish to respond to a changing environment, to compete with introduced (exotic) species and provide greater protection against the threat of extinction than we would expect based on morphology alone.

Indeed, the ability to feed as a generalist may be particularly important in the desert streams and rivers of the southwestern United States. These stream systems historically experience pe-

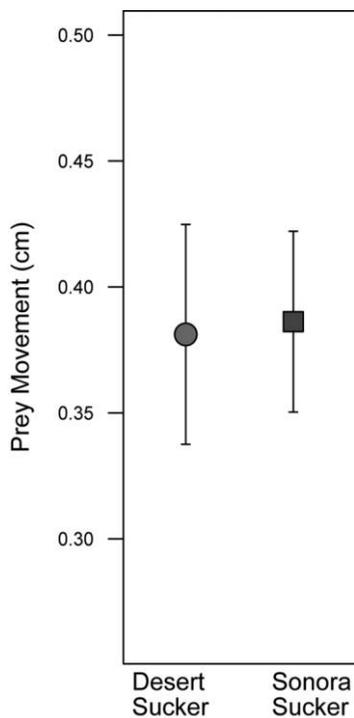


Figure 7. Desert suckers (circle) and Sonora suckers (square) are equally effective in drawing prey into their mouths from the water column when presented with midwater unattached prey. Prey movement for each species is given as the mean value \pm 1 SEM. A color version of this figure is available online.

riodic disturbances and seasonal variation in many abiotic parameters, including water velocity, temperature, and turbidity (Grimm et al. 1997; Stanley et al. 1997; Bogan and Lytle 2006). Such environmental changes will alter key abiotic factors, including temperature and flow (Wigley 2000; Houghton 2001), that determine what food is available within the stream (Hart and Finelli 1999). For example, seasonal environmental changes can trigger cyclic changes in algal blooms and detrital input, which will (in turn) trigger associated changes in the invertebrate community (Thompson and Townsend 1999; Bogan and Lytle 2006). Invertebrate emergence also varies with temperature and season (Bogan and Lytle 2006) and longer-scale periodic cycles or shifts in climate can cause variation in precipitation and ambient temperature (Botkin et al. 2007). These patterns of periodic disturbance and cyclic seasonality in desert streams may have placed selective pressure on aquatic species to develop a specialized morphology that allows them to procure and exploit challenging prey items during periods of food scarcity (Liem 1990). However, it is also possible that overspecialization could prevent a species from exploiting certain prey items, which would place desert fishes at a greater risk of extinction (Olden et al. 2008; Arena et al. 2012). Thus, the ability to modulate feeding behavior may play a key and until now underappreciated role in determining whether the en-

demically fishes of the southwestern United States can adapt to environmental change.

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