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Sensory basis for detection of benthic prey in two Lake Malawi cichlids

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ABSTRACT

The adaptive radiations of African cichlids resulted in a diversity of feeding morphologies and strategies, but the role of sensory biology in prey detection and feeding ecology remains largely unexplored. Two endemic Lake Malawi cichlid genera, *Tramitichromis* and *Aulonocara*, feed on benthic invertebrates, but differ in lateral line morphology (narrow and widened lateral line canals, respectively) and foraging strategy. The hypothesis that they use their lateral line systems differently was tested by looking at the relative contribution of the lateral line system and vision in prey detection by *Tramitichromis* sp. and comparing results to those from a complementary study using *Aulonocara stuartgranti* (Schwalbe et al., 2012). First, behavioral trials were used to assess the ability of *Tramitichromis* sp. to detect live (mobile) and dead (immobile) benthic prey under light and dark conditions. Second, trials were run before, immediately after, and several weeks after chemical ablation of the lateral line system to determine its role in feeding behavior. Results show that *Tramitichromis* sp. is a visual predator that neither locates prey in the dark nor depends on lateral line input for prey detection and is thus distinct from *A. stuartgranti*, which uses its lateral line or a combination of vision and lateral line to detect prey depending on light condition. Investigating how functionally distinctive differences in sensory morphology are correlated with feeding behavior in the laboratory and determining the role of sensory systems in feeding ecology will provide insights into how sensory capabilities may contribute to trophic niche segregation.

1. Introduction

The mechanosensory lateral line system of fishes plays critical roles in prey detection, predator avoidance, communication, rheotaxis, and navigation around obstacles (reviewed in Webb et al., 2008; Bleckmann and Zelick, 2009). The system demonstrates a considerable degree of morphological variation among bony fishes (Webb, 1989b), but understanding the relationship between structure and function in the lateral line system and lateral line-mediated behavior continues to be a particularly challenging task because of the multiple levels at which both structure and function may vary.

The physiological response of the lateral line system (and ultimately the fish's behavior) depends on the properties of the different morphological components that define the system. Variation in the morphology of the neuromasts (hair cell morphology, density, and orientation; neuromast shape; shape and length of the cupula into which the apical ciliary bundles of the hair cells are embedded; and patterns of neuromast innervation and central projections), in the morphology of the lateral line canals in which canal neuromasts are found (canal diameter, pore size, presence of canal constrictions), and in the hydrodynamic context (biotic, abiotic, and self-generated flows) in which the system functions may all contribute to physiological, and thus behavioral, responses (reviewed in Webb, 2014). Ecological correlates of lateral line morphology have been proposed (Dijkgraaf, 1963; reviewed by Webb, 1989b), but there are notable exceptions. For instance, fishes in hydrodynamically active environments tend to have narrow canals and fewer superficial neuromasts, but this relationship does not always hold in light of different sets of selection pressures (Carton and Montgomery, 2004). In addition, some types of morphological variation (differences in canal diameter in the vicinity of canal neuromasts) do not result in differences in physiological responses by neuromasts (e.g., Antarctic notothenioids: Coombs and Montgomery, 1992; Montgomery et al., 1994).

Testing hypotheses concerning the functional evolution of the lateral line system requires that experiments be carried out in a well-defined comparative context using closely related species pairs with divergent morphology and the presentation of ecologically relevant stimuli. Narrow and widened cranial lateral line canals, two of the four types of lateral line canals defined among teleosts (Webb, 1989a), are of particular interest because of their distinctive morphologies and contrasting functional properties (theoretical and experimental work of Denton and Gray, 1988,

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1989). Narrow canals are well ossified with small canal pores and widened canals are typically weakly ossified with partial ossification of the canal roof over the canal neuromasts leaving large canal pores between neuromast positions that are covered by a tympanum-like epithelium typically pierced by very small pores. Narrow canals are widespread among teleosts, while widened canals have evolved convergently in just a dozen or so teleost families suggesting that the evolution of widened canals is adaptive, and further, that it represents an adaptation for prey detection.

The ability to determine the functional distinctions between narrow and widened canals has been hampered by the inability to identify appropriate species pairs that are accessible for experimental study. The percid fishes are a useful model system for illustrating the relationship between the functional morphology of the lateral line system and feeding ecology of fishes. European perch (*Perca fluviatilis*) and yellow perch (*Perca flavescens*) have narrow canals and Eurasian ruffe (*Gymnocephalus cernuus*) has widened canals. The sensitivity of the large neuromasts in the widened canals of ruffe (van Netten, 2006) generally supports behavioral and ecological findings. European perch and ruffe have some seasonal and life stage-dependent diet overlap in their native habitat where they co-occur (Rezsu and Specziar, 2006; Schleuter and Eckmann, 2008), but ruffe occupy a greater depth range than perch and spend more time close to the substrate (Bergman, 1987, 1991). In addition, ruffe are able to feed more successfully in visually compromised habitats when compared to *Perca* spp. (Disler and Smirnov, 1977; Bergman, 1988; Janssen, 1997; Schleuter and Eckmann, 2006) and increase in abundance and replace perch in turbid water and/or low light conditions (Bergman, 1991). Interestingly, the accidental introduction of ruffe in the North American Great Lakes has generated concern over potential for competition with native yellow perch (*P. flavescens*, Ogle et al., 1995).

The speciose cichlids of the African Rift Lakes provide new opportunities for comparative studies of sensory biology, feeding behavior, and ecology. There has been intense study of the functional morphology of the cichlid feeding apparatus and the diverse trophic niches that they occupy (Fryer and Iles, 1972; Liem, 1973, 1980; Albertson et al., 2005; Hulsey et al., 2010), but only a few studies have addressed the sensory basis for prey detection (Hofmann et al., 2009; O'Quin et al., 2010; Mogdans and Nauroth, 2011; Schwalbe et al., 2012). The vast majority of cichlid species have narrow cranial lateral line canals (e.g., Branson, 1961; Peters, 1973; Webb, 1989b). However, a few genera in Lake Tanganyika (*Aulonocranus* and *Trematocara*) and in Lake Malawi (*Aulonocara*, *Alticorpus*, and *Trematocranus*) have widened canals (Konings, 2007).

One of these genera, *Aulonocara* (16–20 spp.), and a genus with narrow canals, *Tramitichromis* (~6 spp.), are found at either the rock–sand interface or over sand, and feed on invertebrates buried in the sand (Fryer and Iles, 1972; Konings, 2007), but use different prey search strategies. *Tramitichromis* plunge into the substrate filling their mouths with sand, and sift out invertebrate prey using their gill rakers ("sand sifting"; Fryer, 1959). How they choose to direct their plunges, and thus the sensory basis for the detection of their benthic prey, is still unknown. In contrast, *Aulonocara stuartgranti* swims just above the substrate, detect water flows generated by prey with their lateral line system (as confirmed with cobalt chloride ablations), and strike at individual prey in the sand (Konings, 2007; Schwalbe et al., 2012). With respect to lateral line morphology, the narrow canals of *Tramitichromis* spp. are well ossified with small pores while the widened canals of *Aulonocara* spp. have large canal pores covered by an epithelium pierced by small perforations. A recent analysis of neuromast morphology in juvenile *Tramitichromis* sp. and *A. stuartgranti* (Becker, 2013) has shown that these fishes have the same number of canal neuromasts and canal pores, despite distinct differences in canal and pore morphology (Fig. 1). They also have the same number of linear series or clusters of very small superficial neuromasts on the head, but late-stage juvenile (and presumably adult) *A. stuartgranti* tend to have more superficial neuromasts within some of these series. The canal neuromasts are diamond-shaped in both species, but those in *A. stuartgranti* are a bit larger (Fig. 1B) and tend to sit in slight constrictions in the canal, which is a characteristic of many species with widened canals.

Thus, *Tramitichromis* sp. and *A. stuartgranti* present an excellent model system in which to ask questions about the relationship of lateral line morphology to its role in prey detection. These fish differ with respect to only some aspects of the morphology of the lateral line system (narrow vs. widened canals, minor differences in canal neuromast size, and the number of superficial neuromasts). Experimental work has already determined that the lateral line system is critical for prey detection in *A. stuartgranti* (Schwalbe et al., 2012) and it is hypothesized that the role of the lateral line system in prey detection in *Tramitichromis* sp. would be different from that in *A. stuartgranti*. In order to test this, behavioral trials (as described in Schwalbe et al., 2012) were conducted in which *Tramitichromis* sp. was presented with live (mobile) and dead (immobile) tethered adult brine shrimp under light and dark conditions (Experiment I). Then, the role of the lateral line system in prey detection was directly addressed by temporarily inactivating the lateral line system with cobalt chloride (Experiment II). Data on number of prey strikes, prey detection distance and angle and preference for live or dead prey were then compared with that for *A. stuartgranti* (data from Schwalbe et al., 2012) to contrast the roles of the lateral line system and vision in prey detection behavior in these two species.

2. Materials and methods

2.1. Study species

Adult *Tramitichromis* sp. (=*Tramitichromis* hereafter, unless otherwise noted) were acquired from a commercial supplier (Old World Exotic Fish, Inc., Homestead, FL, USA) and housed in small groups in 190 l aquaria with mechanical and biological filtration. For housing and experimental procedures, fish were maintained at 1 ppt salt (Cichlid Lake Salt; Seachem Laboratories, Inc., Madison, GA, USA) at 26 ± 1 °C with a 12:12 h light:dark cycle. Fish were fed daily with cichlid pellets (New Life Spectrum Cichlid Formula; New Life International, Inc., Homestead, FL, USA) and supplemented with live adult brine shrimp. Animal care and all experimental procedures followed an approved University of Rhode Island IACUC protocol.

2.2. Behavioral trials

Two experiments were conducted to determine the ability of *Tramitichromis* to detect live and dead prey in light and dark trials (Experiment I) and to determine the contribution of the lateral line system to prey detection in light trials (Experiment II).

2.2.1. Experiment I – light and dark trials

Light and dark trials were conducted using *Tramitichromis* following Schwalbe et al. (2012). Briefly, trials were performed in a large experimental tank (375 l) lined with sand. Adult brine shrimp (*Artemia* sp.) were tethered with elastic thread in pairs (1 live; 1 dead, freshly frozen) onto each one of six mesh platforms (a total of 6 live prey + 6 dead prey = 12 total prey) to serve as a proxy for naturally occurring benthic prey. Platforms were placed on the bottom of the tank in a 2 × 3 grid so that their top surfaces were flush with that of the sand. All filters in the experimental tank were turned off to eliminate hydrodynamic noise during all behavioral trials.

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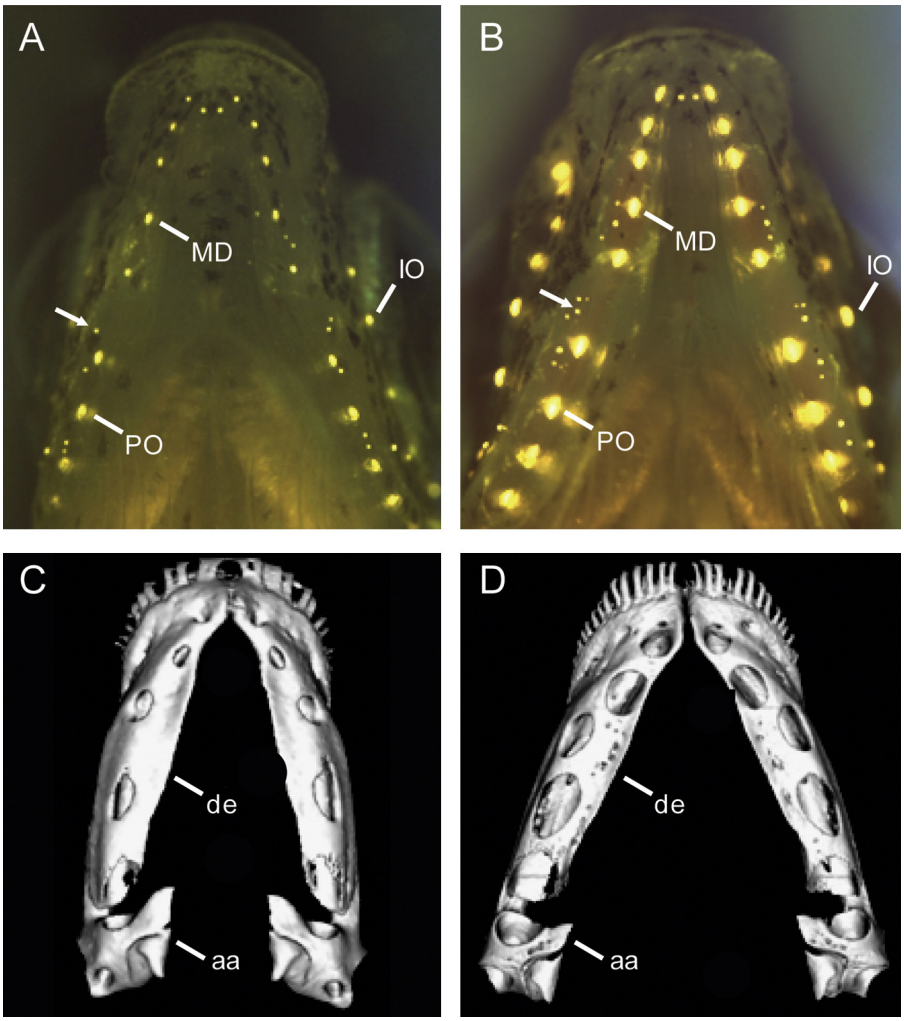

Fig. 1. Ventral view of the mandible of *Tramitichromis* sp. and *Aulonocara* spp. illustrating the canal and superficial neuromasts and mandibular lateral line canals. Top: Ventral view of (A) a juvenile *Tramitichromis* sp. (standard length [SL] = 18 mm) and (B) *A. stuartgranti* (SL = 16 mm) fluorescently stained with 4-Di-2-ASP (63 μM, 5 min) to reveal the hair cells in the sensory strip in superficial neuromasts (lines and clusters [arrows]) and larger canal neuromasts in the mandibular (MD), preopercular (PO), and infraorbital (IO) canals. Bottom: MicroCT 3-D reconstruction of the mandible (dentary [de] and angulo-articular [aa] bones) of (C) *Tramitichromis* sp. (SL = 29 mm) showing the bony pores of the MD canal and (D) *A. baenschi* (SL = 87 mm).

At the start of a trial, a fish was released from behind an opaque barrier into the experimental arena and recorded for 30 min using a HD digital video camera (HDR-CX550V, 30 frames per second; Sony Corp., Tokyo, Japan) mounted directly above the tank. Light trials were carried out under standard white fluorescent illumination and dark trials were conducted under infrared (IR) illumination (IR-200/24, peak = 840 nm; Speco Provideo, Amityville, NY, USA). Each of six naïve male fish (total length [TL] = 99–110 mm) was run sequentially through 3 light and then 3 dark trials for a total of 18 light trials and 18 dark trials. Each trial was performed on a different day, and trials were carried out over the course of five months with a mean time between the first light trial and last dark trial of 19 days for an individual fish. Several additional light and dark trials were recorded in lateral view to observe the fishes' position relative to the substrate.

2.2.2. Experiment II – chemical ablation of the lateral line system

In order to determine the role of the lateral line system in prey detection by *Tramitichromis*, fish were treated with cobalt (II) chloride heptahydrate (cobalt chloride; Sigma–Aldrich, St Louis, MO, USA) to deactivate the lateral line system as in Schwalbe et al. (2012). The results of Experiment I (Section 3.1) demonstrated that while all fish were active during dark trials, the majority of fish did not feed in the dark, so Experiment II consisted only of light trials. Each one of three fish (all males, not used in Experiment I; TL = 92–98 mm) was run through a sequence of three different trials. First, a 30 min "pre-cobalt" trial (identical to the light trials in Experiment I) was carried out to establish a behavioral baseline. Two to three days later, the fish was treated in a large container filled with 0.1 mM cobalt chloride in conditioned tap water for 3 h (calcium = 60 mg/l) (Hach hardness test kit; Hach Co., Loveland, CO, USA) and returned to the experimental tank (calcium = 260 mg/l). When the fish appeared to be behaving normally (i.e., normal respiration and swimming, about 2 h after cobalt treatment), a "cobalt trial" was conducted. All fish resumed feeding on commercial pellets and/or live brine shrimp immediately following cobalt trials. After 21 days (in the experimental tank), the fish was run through a "post-cobalt" trial to assess recovery from cobalt treatment and allow a comparison with the "pre-cobalt" and "cobalt" trials. In a previous study (Schwalbe et al., 2012), the effect of handling was assessed by running fish through one light and dark trial a few days before and immediately after a sham cobalt chloride treatment (=4 trials/fish). For the sham treatment, fish ($n = 2$) were placed in a large container of conditioned tap water for 3 h instead of the cobalt

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chloride solution. Fish consumed prey during both light and dark trials before and after sham treatment, so it appeared that handling had no effect on feeding behavior.

2.3. Data analysis

At the end of each trial, remaining prey were counted to determine the number and type of prey (live and dead) that had been consumed and strike success was also confirmed in video recordings. Video recordings were analyzed using Premier Pro (CS5; Adobe Systems Inc., San Jose, CA, USA) and images from video sequences of prey detections (e.g., when the fish oriented towards the prey) to prey strikes were exported for further analysis. These images were used to identify when detections occurred relative to the start of the trial, during which phase of the saltatory search strategy each prey was detected (defined by O'Brien et al., 1989; a cycle of three swimming phases – caudal fin thrust, glide and pause), and the order of prey strikes (live vs. dead) as an approximation of "prey preference". In addition, detection distance and detection angle for each strike were measured from the images using ImageJ v. 1.41o (Rasband, 1997–2012).

All data were tested for normality (Kolmogorov–Smirnov test) and only detection distance data needed to be $\log_{10}$ transformed to achieve normality. Separate tests using a generalized linear mixed model (GLMM) (SPSS, v.19) with pairwise post hoc comparisons (least significant differences, LSD) were used to detect differences in four variables (number of prey strikes, detection distance, swimming phase in which strikes occurred, and order of prey capture) with reference to prey type (live vs. dead) and light condition (light vs. dark). This approach allowed the selection of random (individual) and fixed effects (species, light condition, prey type) while addressing repeated measures for the same individual. Prey preference was calculated using a method described in Taplin (2007) in which prey preference was assessed by ranking the prey according to the order in which they were consumed, and then calculating a preference score by taking the mean of the order values for each prey type. Necessary assumptions for this analysis were satisfied: multiple types of prey were offered simultaneously (e.g., live and dead tethered brine shrimp) and prey consumed last could not be distinguished from uneaten prey. Scores closer to 1 indicate a strong preference, whereas scores closer to 12 (=total number of prey offered) indicate no preference or rejection. Preference scores for live or dead prey in each light condition (light, dark) were compared using paired *t*-tests. Means of prey preference scores from the three replicate trials carried out for each fish were calculated prior to performing the paired *t*-test, so that the replicate variable was the fish (individual) and not the trial. Finally, Watson's U^2-tests (Oriana v.3; Kovach Computing Services, Pentraeth, UK) were used to analyze differences in detection angles with reference to prey type and light condition. Differences were considered to be significant at the level $P < 0.05$ for all statistical tests. Values are given as mean ± SE unless otherwise specified.

3. Results

Experiments I and II showed that *Tramitichromis* is a visual predator that does not seek out prey in the dark and does not depend on its lateral line system for detection of benthic invertebrate prey in light trials. *Tramitichromis* is thus quite distinct from *A. stuartgranti*, which relies on the interaction of vision and lateral line for prey detection and uses the lateral line system for detection of prey in the dark (Schwalbe et al., 2012).

3.1. Experiment I – light and dark trials

Tramitichromis explored the tank by moving throughout the vertical extent of the water column. After the first prey detection, fish generally swam within ~10 cm of the sand and struck at and removed prey from the platforms. Fish alternated between moving around the entire tank (vertically and horizontally) and swimming close to the sand, even after all 12 tethered brine shrimp had been captured. Sand sifting was frequently observed during trials and after all prey items had been consumed.

In light trials, all *Tramitichromis* successfully struck at and consumed prey (94.4% of total prey presented) but fish attacked more live prey than dead prey (LSD, $P = 0.005$; Table 1, Fig. 2A). Strikes on live prey preceded those on dead prey (paired *t*-test, $t_5 = 8.851$, $P < 0.001$; Table 2) and live prey were detected at a greater distance than dead prey (live = 11.3 ± 0.5 cm, dead = 9.0 ± 0.5 cm; LSD, $P = 0.002$; Table 1, Fig. 3A). Prey was detected non-uniformly around the fishes' bodies (Rayleigh test, $Z = 107.98$, $P < 0.001$; Fig. 4A) and all fish detected prey in the same relatively narrow range in front of the snout (±40° from the body axis; Watson's U^2-test, $P > 0.05$). *Tramitichromis* demonstrated a saltatory search strategy (cyclic sequence of caudal fin thrust, glide, and pause), and more prey strikes (live and dead prey combined) were initiated during a pause (77.3%) than during a glide (22.7%) and never during a thrust (Fig. 5A).

The results of dark trials were quite different. The median number of strikes was zero for both live and dead prey, which greatly contrasts with the median number of six strikes in light trials (for live or dead prey offered; Fig. 2A). All fish actively swam around the tank in dark trials as they did in light trials and some exhibited sand sifting behavior. A few strikes did occur during dark trials, but one fish was responsible for 21 of the total 23 strikes (on 216 live and dead prey presented in 18 trials). When comparing strikes on live and dead prey, no significant differences were detected in any of the measured variables used to describe prey detection behavior (e.g., prey preference, Table 2; number of prey strikes, Fig. 2A; detection distance, Fig. 3A; detection angle, Fig. 4A; and swimming phase at prey detection, Fig. 5A), indicating that live prey could not be distinguished from dead prey.

However, when comparing the few strikes that did occur in dark trials ($n = 23$) to the numerous strikes in light trials ($n = 204$; Fig. 2A), significant differences were observed in some aspects of behavior. In dark trials, prey were detected at shorter distances than in light trials (live and dead combined: light = 10.3 ± 0.4 cm,

Table 1
Generalized linear mixed model results for *Tramitichromis* feeding on live and dead prey during light and dark trials (Experiment I) comparing number of prey strikes, detection distance, and swimming phase during prey detection (pause vs. glide).

Source	Number of prey strikes			Detection distance			Pause vs. glide		
	F	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
Light/dark	273.28	1, 68	<0.001	40.89	1, 213	<0.001	10.39	1, 213	0.001
Prey	3.83	1, 68	n.s.	2.52	1, 213	n.s.	1.29	1, 213	n.s.
Light/dark × prey	4.68	1, 68	0.034	0.25	1, 213	n.s.	0.003	1, 213	n.s.

n.s., not significant.

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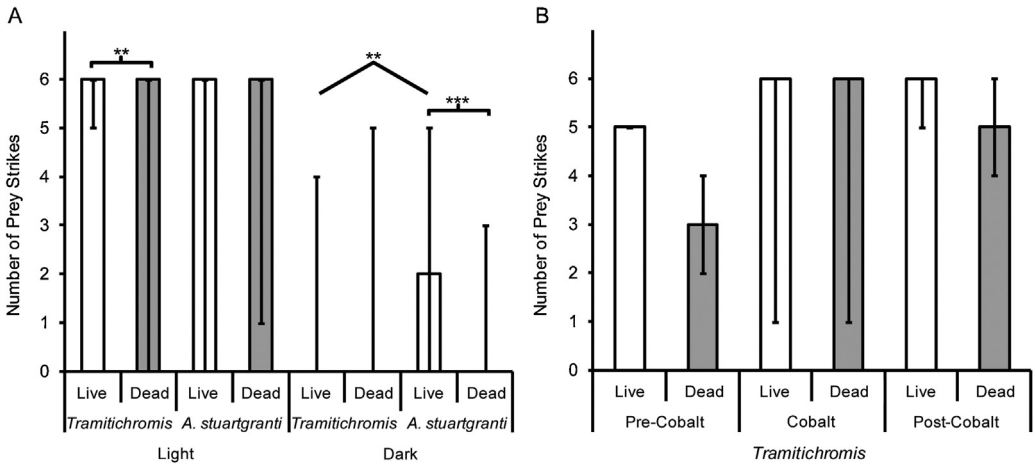

Fig. 2. Number of prey strikes (median ± min/max) on live and dead prey for (A) *Tramitichromis* (Experiment I) and *A. stuartgranti* (data from Schwalbe et al., 2012) in light and dark trials, and (B) *Tramitichromis* (Experiment II, light trials only). LSD, $^{**}P < 0.01$, $^{***}P < 0.001$. See text for additional details.

Table 2
Mean prey preference scores for *Tramitichromis* (Experiments I and II) and *Aulonocara stuartgranti* (Experiment I only, data from Schwalbe et al., 2012) feeding on live and dead prey in light and dark (Experiment I only) trials following Taplin (2007). If the fish demonstrated a preference for a type of prey (indicated by a significant lower preference score), it was always for live prey (paired *t*-test).

Species	Experiment		Light trials		Dark trials	
			Live	Dead	Live	Dead
Tramitichromis	Experiment I		5.74***	7.26	6.54	6.46
A. stuartgranti			5.49**	7.52	4.78**	8.22
Tramitichromis	Experiment II	Pre-cobalt	5.25*	7.75		
		Cobalt	6.08	6.92		
		Post-cobalt	6.67	6.33		

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

dark = 2.3 ± 0.3 cm; LSD, $P < 0.001$; Table 1, Fig. 3A) and more prey were detected during a glide in dark trials (60.9% of strikes) than in light trials (22.7% of strikes; LSD, $P = 0.002$, Table 1, Fig. 5A). Even though prey were detected in a wide range of angles around the body during dark trials, the majority of prey were detected in the same narrow range of angles as in light trials (±40° from body axis, Watson's U^2-test, $P > 0.05$, Fig. 4A). While differences were observed in several behavioral parameters in light and dark trials, *Tramitichromis* tended not to feed in the dark and when they did, prey appeared to be found rather randomly as fish explored the experimental arena.

3.2. Experiment II – chemical ablation of the lateral line system

The results for all trials of Experiment II – before (pre-cobalt trials), immediately following (cobalt trials), and three weeks after treatment with cobalt chloride (post-cobalt trials) – were comparable to the results for light trials in Experiment I. All fish actively

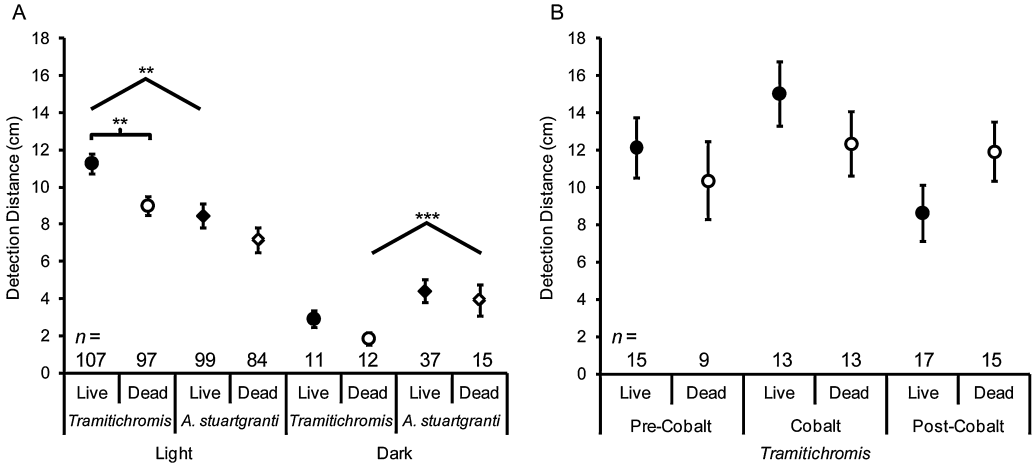

Fig. 3. Detection distance (mean ± SE) for live and dead prey for (A) *Tramitichromis* (Experiment I) and *A. stuartgranti* (data from Schwalbe et al., 2012) in light and dark trials, and (B) *Tramitichromis* sp. (Experiment II, light trials only). Non-transformed data are illustrated here (which are biologically relevant), but statistics were carried out on log-transformed data, as appropriate. LSD, $^{**}P < 0.01$, $^{***}P < 0.001$. See text for additional details.

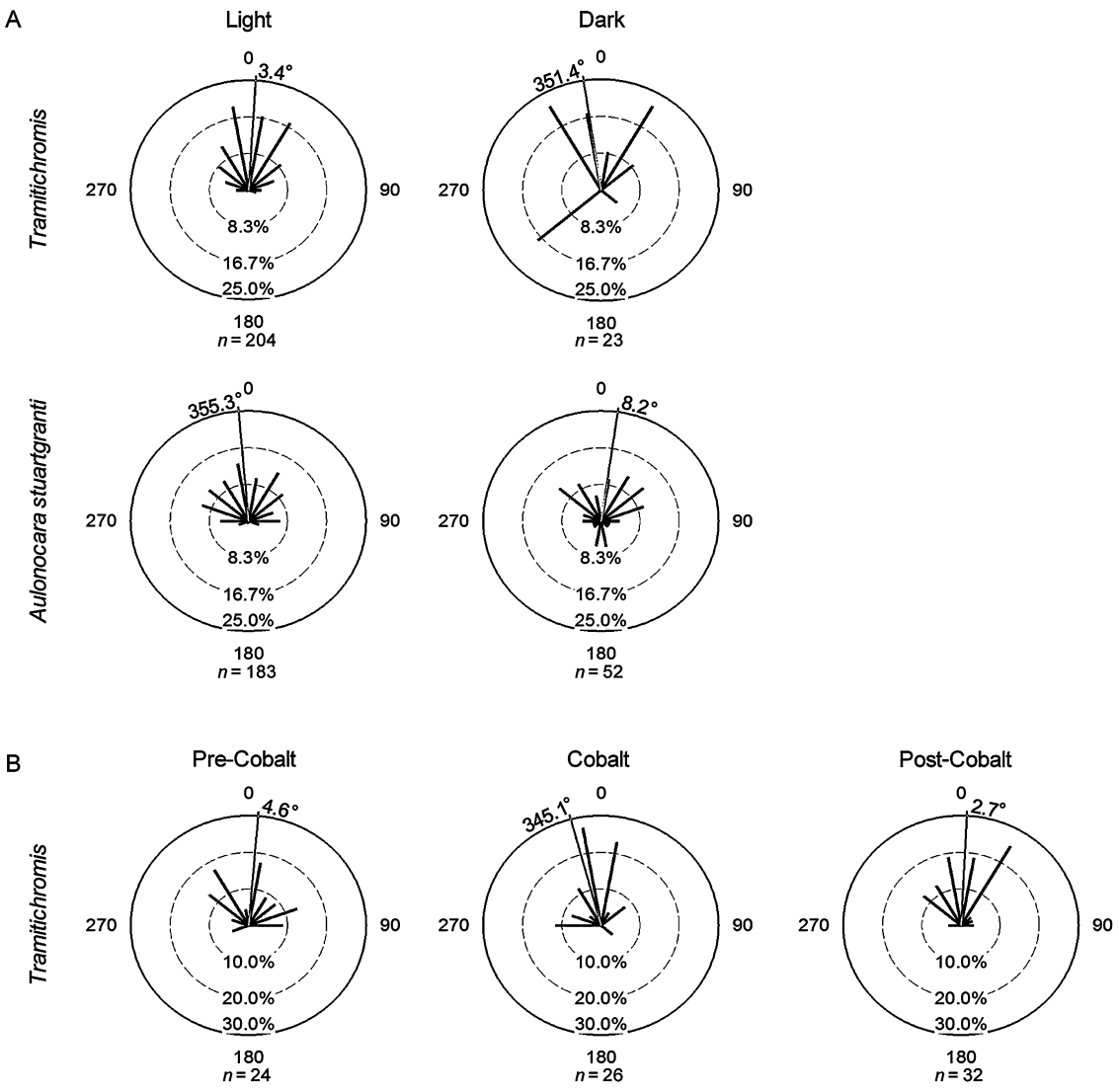

Fig. 4. Orientation to prey (live and dead combined) at time of detection for (A) *Tramitichromis* (Experiment I) and *A. stuartgranti* (data from Schwalbe et al., 2012) light and dark trials and (B) *Tramitichromis* (Experiment II, light trials only). Bars represent the proportion of the total number of detection events grouped into 20° intervals. The narrow line represents mean angle. The center of the polar plot (facing 0°) represents the location of the midpoint between the eyes. See text for additional details.

swam around the experimental arena and consumed the majority of live and dead prey presented in pre-cobalt (66.7% of total prey presented), cobalt (72.2%), and post-cobalt recovery (88.9%) trials. The total number of strikes on live and dead prey was the same among the three trial types (GLMM, $P > 0.05$; Table 3, Fig. 2B). Live and dead prey were detected from similar distances in all of these trials (Table 3; Fig. 3B). Prey were detected non-uniformly around the body in all trials (Rayleigh test, $P < 0.04$; Fig. 4B) and detection angle did not vary with prey type or among sequential trials (Watson's U^2-test, $P > 0.05$), just like in Experiment I light

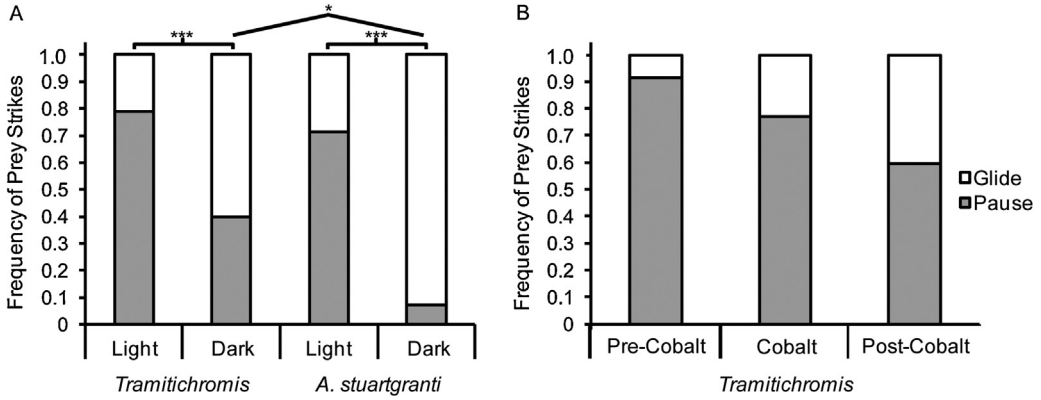

Fig. 5. Frequency of prey detections that occurred during the glide or pause phase of swimming leading to prey strikes in (A) *Tramitichromis* (Experiment I) and *A. stuartgranti* (data from Schwalbe et al., 2012) light and dark trials, and (B) *Tramitichromis* (Experiment II, light trials only). LSD, $^{*}P < 0.05$, $^{***}P < 0.001$. See text for additional details.

Table 3
Generalized linear mixed model results for *Tramitichromis* feeding on live and dead prey during light trials after cobalt chloride treatment (Experiment II) comparing number of prey strikes, detection distance, and swimming phase during prey detection (pause vs. glide).

Source	Number of prey strikes			Detection distance			Pause vs. glide		
	F	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
Trial	1.38	2, 12	n.s.	2.24	2, 76	n.s.	0.000	2, 75	n.s.
Prey	2.87	1, 12	n.s.	0.07	1, 76	n.s.	0.001	1, 75	n.s.
Trial × prey	0.96	2, 12	n.s.	1.95	2, 76	n.s.	0.000	2, 75	n.s.

n.s., not significant.

Table 4
Generalized linear mixed model results for *Tramitichromis* (this study) and *Aulonocara stuartgranti* (data from Schwalbe et al., 2012) feeding on live and dead prey during light and dark trials (Experiment I) comparing number of prey strikes, detection distance, and swimming phase during prey detection (pause vs. glide).

Source	Number of prey strikes			Detection distance			Pause vs. glide		
	F	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
Species	0.38	1, 136	n.s.	2.34	1, 444	n.s.	0.000	1, 432	n.s.
Light/dark	352.89	1, 136	<0.001	156.46	1, 444	<0.001	0.000	1, 432	n.s.
Prey	12.46	1, 136	0.001	6.24	1, 444	0.013	0.003	1, 432	n.s.
Light/dark × prey	0.40	1, 136	n.s.	0.12	1, 444	n.s.	0.000	1, 432	n.s.
Species × light/dark	7.69	1, 136	0.006	23.17	1, 444	<0.001	0.000	1, 432	n.s.
Species × prey	1.29	1, 136	n.s.	4.45	1, 444	0.036	0.003	1, 432	n.s.
Species × light/dark × prey	4.07	1, 136	0.046	2.11	1, 444	n.s.	0.000	1, 432	n.s.

n.s., not significant.

trials. In pre-cobalt trials, live prey were captured before dead prey (paired *t*-test, $t_2 = 8.66$, $P = 0.013$), but this preference for live prey was absent in cobalt trials and post-cobalt trials ($P > 0.05$; Table 2). As in the light trials in Experiment I, most prey were detected during a pause, and the frequency of prey detection during a pause or glide did not differ among the pre-cobalt, cobalt, and post-cobalt trials (GLMM, $P > 0.05$; Table 3, Fig. 5B).

3.3. *Comparison of feeding behavior in* Tramitichromis *and* Aulonocara stuartgranti

Interesting similarities and contrasts were found in prey detection behavior in *Tramitichromis* and *A. stuartgranti*. Both species swam around the tank in light and dark trials using a saltatory search strategy, but *Tramitichromis* tended to swim higher above the sand while searching for prey and pitched forward more (i.e., ~45° vs. ~30° for *A. stuartgranti*) during prey strikes. In addition, *Tramitichromis* did not demonstrate the swimming reversals (i.e., swimming backwards) upon prey detection that *A. stuartgranti* did, and *A. stuartgranti* did not use the sand sifting strategy used by *Tramitichromis*.

In light trials, *Tramitichromis* and *A. stuartgranti* detected similarly high numbers of live and dead prey (GLMM, $P > 0.05$; Table 4, Fig. 2A), and both demonstrated a preference for live prey (*Tramitichromis*: paired *t*-test, $t_5 = 8.851$, $P < 0.001$; *A. stuartgranti*: paired *t*-test, $t_5 = 5.551$, $P = 0.003$; Table 2). In addition, both species detected more prey during a pause rather than during a glide, and did so with frequencies that were not statistically different (GLMM, $P > 0.05$; Table 4, Fig. 5A). *Tramitichromis* detected live prey at longer distances than *A. stuartgranti* (LSD, $P = 0.006$; Fig. 3A), but both species detected dead prey at distances that were not statistically different ($P > 0.05$). Detection angles were significantly different for *Tramitichromis* and *A. stuartgranti* (Watson U^2-test, $U^2 = 0.468$, $P < 0.001$; Fig. 4A); *Tramitichromis* detected the majority of prey in a narrower range of angles (±40° from body axis) than did *A. stuartgranti* (±90° from body axis).

In dark trials, *Tramitichromis* also demonstrated different prey detection behaviors than *A. stuartgranti*. Only half of the *Tramitichromis* individuals ($n = 3$ of 6 fish) struck at prey while all *A. stuartgranti* ($n = 6$ fish) struck at prey. When prey was detected, *Tramitichromis* struck at fewer live prey than did *A. stuartgranti* (LSD, $P = 0.006$), but the number of strikes on dead prey was not statistically different in the two species ($P > 0.05$; Fig. 2A). Furthermore, although both species tended to detect more prey during a glide than during a pause in dark trials, *Tramitichromis* detected fewer prey during a glide than did *A. stuartgranti* (LSD, $P = 0.020$; Fig. 5A). In addition, *Tramitichromis* detected prey at shorter distances than did *A. stuartgranti* (both prey types combined, LSD, $P < 0.001$; Fig. 3A). Detection angles were not statistically different in dark trials (Watson's U^2-test, $P > 0.05$) and both species found prey non-uniformly around their bodies (Fig. 4A).

4. Discussion

The results of Experiments I and II showed that the combination of lateral line, olfactory, and tactile cues was not sufficient to elicit a prey strike response by *Tramitichromis* in the absence of visual cues, but that in light trials a combination of sensory inputs may provide some additional information when used in tandem with vision. This study demonstrated that closely related taxa that feed on the same prey in the same sensory environment, but have two morphologically (and likely functionally) distinct lateral line systems, use different sensory systems to detect their prey under different light conditions in the laboratory.

4.1. *Feeding behavior of* Tramitichromis

The experimental design in Experiments I and II ensured that different combinations of sensory cues were available to the fish allowing multimodal sensory input to be considered in the interpretation of the results. In Experiment I light trials, all stimuli generated by the movement of the brine shrimp were present and all sensory systems in *Tramitichromis* were intact (i.e., vision, lateral line system, olfaction). In addition, the significance of prey movements for prey detection – the visual motion stimulus, hydrodynamic flow, and spread of an odor plume generated by the motion of the brine shrimp – was addressed by providing both live and dead prey in all trials. Visual cues were absent in dark trials in Experiment I, but lateral line and olfactory systems were still intact (hydrodynamic and olfactory cues were available). In Experiment II (light trials only), the ability to detect hydrodynamic cues was eliminated by temporarily inactivating the lateral line

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system by treatment with cobalt chloride, but visual and olfactory cues were still available. A dependence on more than one sensory modality was inferred when feeding behavior was not as robust in trials in which input to one or more sensory modalities was eliminated compared to trials in which all sensory systems were available.

Tramitichromis demonstrated the most robust feeding behavior when all sensory cues were available (Experiment I light trials). In these trials, *Tramitichromis* demonstrated a preference for live prey, which were detected from greater distances than were dead prey. The visual motion stimulus generated by live brine shrimp likely strengthened the visual stimulus necessary for prey detection and was responsible for the generation of robust prey detection behavior at longer distances. More prey detections occurred during a pause than a glide in light trials, when the prey could be localized in a more stable visual field. Even though the olfactory system was intact and olfactory cues were available during light and dark trials in Experiments I and II, behaviors characteristic of olfactory-mediated prey detection (e.g., following and/or locating the source of an odor by zig-zagging through its odor plume; Hara, 1993) were not observed. These results all indicate that visual detection of prey is critical for feeding in *Tramitichromis*, and that they were relatively unsuccessful in detecting prey in dark trials likely because they could not see the prey. Finally, in Experiment II, feeding behavior was similar before, immediately following, and after the recovery from lateral line ablation using cobalt chloride, providing evidence that *Tramitichromis* does not appear to depend on its lateral line system for prey detection. Morphological confirmation of lateral line ablation by cobalt chloride was accomplished by fluorescently staining three juvenile *Tramitichromis* with 4-Di-2-ASP (63 μM, 5 min; also see Fig. 1) following a 3 h treatment with either cobalt chloride in calcium free tank water (0.1 mM), or only in calcium free tank water as a control (Becker, 2013). A lack of hair cell staining in the central region of the neuromasts in *Tramitichromis* was similar to that observed in juvenile *A. stuartgranti* treated with cobalt chloride (0.05 and 0.1 mM, Schwalbe et al., 2012).

Tramitichromis feeds on benthic invertebrates in the sand at the rock–sand interface in Lake Malawi (Fryer, 1959; Konings, 2007), a community that is dominated by Ostracoda, Hydracarina, and Chironomidae larvae and also includes hydropsychid caddisfly, heptageneid mayfly, and dryopoid beetle nymphs (Abdallah and Barton, 2003). *Tramitichromis* is known for plunging into the sand, engulfing a mouthful of sand, and sifting it through their gill rakers, but how they determine where to initiate this behavior is not known. Given the results of the current study, it is likely that the fish can see minute changes in the substrate (e.g., a slightly exposed invertebrate or movements by invertebrates in the substrate), perhaps in combination with olfactory cues, to find these prey. Tactile cues may also elicit prey strikes and/or sand sifting behavior, but lateral video recordings of behavioral trials suggest otherwise because *Tramitichromis* swam several centimeters above the substrate and tended not to contact the substrate with their pelvic fins.

Finally, the ability of one of the six *Tramitichromis* to detect both live and dead prey in dark trials cannot be easily explained. *Tramitichromis intermedius* has spectral sensitivity peaks that are somewhat higher than those of other Lake Malawi cichlids examined (including *Aulonocara jacobfreibergi*; Parry et al., 2005), but among all retinal cell types, the longest wavelength of maximum absorbance is only about 570 nm (for the double cones). However, two recent studies have demonstrated that cichlids show positive phototactic behavior (*Oreochromis mossambicus*, Shcherbakov et al., 2012) and strong foraging responses (*Pelvicachromis taeniatus*, Meuthen et al., 2012) in near-IR light. Thus, it is possible that this one *Tramitichromis* was able to successfully detect prey in dark trials, which were illuminated with a light source in the near-IR range.

4.2. Comparison of prey detection behaviors in two benthic feeding cichlids

This study has shown that *Tramitichromis* and *A. stuartgranti* use two distinct methods for detecting the same prey, likely due to the different roles of their sensory systems. Both species exhibited a saltatory search strategy (which cycles between moving through an area and pausing to locate prey or repositioning before the next forward movement) and different sensory systems are likely important during a pause or glide, in light and dark trials. Both *Tramitichromis* and *A. stuartgranti* appeared to visually scan for prey during a pause in light trials, when the visual field was stable. In light trials, *Tramitichromis* detected more prey in a narrow range of angles relative to the body axis suggesting that they may possess adequate binocular vision to localize prey (as shown in other teleosts; Sivak, 1978; Bianco et al., 2011; Miyazaki et al., 2011). In contrast, *A. stuartgranti* detected prey in a wider range of angles suggesting that binocular vision was not employed. However, they struck at a higher proportion of prey during a pause in light trials, suggesting that stabilization of the visual field favored successful prey detection. In dark trials, *A. stuartgranti* detected prey as swimming velocity decreased during a glide, allowing localization of prey as it came within the operational range of its lateral line system.

The temporary ablation of the lateral line system with cobalt chloride had different effects on the two species. In *Tramitichromis*, prey detection behavior did not change with the elimination of lateral line input, while in *A. stuartgranti*, there was a reduction in the number of prey strikes in light trials and the elimination of prey detection in dark trials (Schwalbe et al., 2012). It is concluded that *Tramitichromis* does not depend on lateral line input for successful prey detection, in contrast to *A. stuartgranti*, which depends on both vision and the lateral line system in light trials, and uses its lateral line system to detect prey in the dark. The correlation of this behavioral data with the difference in lateral line canal morphology in *Tramitichromis* and *A. stuartgranti* suggests that the widened lateral line canals are an adaptation for prey detection, especially in the absence of visual cues.

4.3. Could sensory biology contribute to the feeding ecology of African cichlids?

There has been a long history of discussion about the role of feeding mechanisms in the definition of cichlid trophic niches (Fryer and Iles, 1972; Liem, 1973, 1980; McKay and Marsh, 1983; Albertson et al., 2003) and the ways in which trophic niche differentiation and ecological segregation occur among African cichlids (Goldschmidt et al., 1990; Reinthal, 1990; Sturmbauer et al., 1992; Hori et al., 1993; Bouton et al., 1997; Genner et al., 1999a,b; Duponchelle et al., 2005; Martin and Genner, 2009; Genner and Turner, 2012). In their landmark monograph, Fryer and Iles (1972) reviewed the feeding biology and evolution of cichlid fishes of the African Rift Lakes, but the ecological concepts of habitat partitioning and mechanisms underlying the evolution of trophic diversity among cichlids has only been examined in detail more recently (reviewed in Genner and Turner, 2005; Albertson, 2008). For instance, within the rock-dwelling mbuna flock, it has been hypothesized that fine-scale niche partitioning occurs among species that forage on a combination of algae, aufwuchs, phytoplankton, and other seasonally available food (Reinthal, 1990; Bouton et al., 1997; Genner et al., 1999b). However, there appears to be a continuum in the degree of niche overlap among these species depending on whether or not shared resources are limiting (Bouton et al., 1997; Genner et al., 1999b; Duponchelle et al., 2005), and a high degree of overlap may

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occur regardless of the availability of shared resources (Martin and Genner, 2009).

Recent field observations by other investigators (Konings, 2007) and results from the current study permit some speculation about the sort of behavioral and ecological interactions that may be occurring between species of *Tramitichromis* and *Aulonocara*. A small number of stomach content analyses show potential for diet overlap in these taxa (Fryer, 1959; Konings, 2007). Species of *Tramitichromis* and *Aulonocara* have lake-wide distributions (Konings, 2007), presenting the opportunity for spatial overlap. Where they co-occur, *Aulonocara* might experience interference competition from *Tramitichromis* given its prey search strategies. For instance, members of these two genera have been observed foraging in the same areas where *Tramitichromis* (and other sand sifters) can interrupt foraging by *Aulonocara* (which hover just above the sand searching for prey) by just swimming nearby (M. Kidd, personal communication). Furthermore, the sand plunging behavior of *Tramitichromis* likely disrupts other invertebrates in the sand, altering the topography of the bottom sediments, which may prevent *Aulonocara* from detecting prey as they swim just above the sand surface. These two taxa also occupy different depth ranges (*Tramitichromis* spp.: <15 m, Konings, 2007; *Aulonocara* spp.: 5–120 m, Konings, 1990, 2007). Species of *Aulonocara* may escape competition in shallower waters by foraging in deeper water. Genner and Turner (2012) assigned several species of *Aulonocara* to an assemblage of "deep benthic feeders" and noted that these fishes have sensory adaptations (including modification of the cranial lateral line canal system) that should enable them to detect prey at the depths at which they are found. This is supported by experimental work that demonstrated that *A. stuartgranti* uses its lateral line system in prey detection, especially in the dark (Schwalbe et al., 2012). Furthermore, the ability of species of *Aulonocara* to detect prey non-visually may allow them to forage crepuscularly and/or nocturnally (not yet documented in the field), thus facilitating spatial and temporal segregation between *Aulonocara* species and other cichlids that feed on benthic invertebrates in the sand, including species of *Tramitichromis*.

Future studies that integrate the analysis of laboratory-based sensory biology with field-based ecological studies will allow tests of the hypotheses (i) that evolutionary changes in the morphology and physiological capabilities of a sensory system (such as widened canals) are adaptations that allow species to occupy novel trophic niches, and (ii) that species use different combinations of sensory cues in the same sensory environment to spatially or temporally partition similar resources in a common habitat.

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References

Abdallah, A.M., Barton, D.R., 2003. Environmental factors controlling the distributions of benthic invertebrates on rocky shores of Lake Malawi, Africa. J. Great Lakes Res. 29, 202–215.
Albertson, R.C., 2008. Morphological diversity predicts habitat partitioning in a Lake Malawi cichlid species complex. Copeia 2008, 689–698.
Albertson, R.C., Streelman, J.T., Kocher, T.D., 2003. Directional selection has shaped the oral jaws of Lake Malawi cichlid fishes. Proc. Natl. Acad. Sci. U.S.A. 100, 5252–5257.
Albertson, R.C., Streelman, J.T., Kocher, T.D., Yelick, P.C., 2005. Integration and evolution of the cichlid mandible: the molecular basis of alternate feeding strategies. PNAS 102, 16287–16292.
Becker, E.A., 2013. The distribution and ontogeny of neuromast receptor organs and a comparison of methods for chemical ablation of the lateral line system in two cichlid fishes. Master's Thesis, University of Rhode Island.
Bergman, E., 1987. Temperature-dependent differences in foraging ability of two percids, *Perca fluviatilis* and *Gymnocephalus cernuum*. Environ. Biol. Fish. 19, 45–54.
Bergman, E., 1988. Foraging abilities and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. J. Anim. Ecol. 57, 443–453.
Bergman, E., 1991. Changes in abundance of two percids, *Perca fluciatilis* and *Gymnocephalus cernuus*, along a productivity gradient: relations to feeding strategies and competitive abilities. Can. J. Fish. Aquat. Sci. 48, 536–545.
Bianco, I.H., Kampff, A.R., Engert, F., 2011. Prey capture behavior evoked by simple visual stimuli in larval zebrafish. Front. Syst. Neurosci. 5, 1–13.
Bleckmann, H., Zelick, R., 2009. Lateral line system of fish. Integr. Zool. 4, 13–25.
Bouton, N., Seehausen, O., van Alphe, J.J.M., 1997. Resource partitioning among rock-dwelling haplochromines (Pisces: Cichlidae) from Lake Victoria. Ecol. Freshw. Fish 6, 225–240.
Branson, B.A., 1961. The lateral-line system in the Rio Grande perch, *Cichlasoma cyanoguttatum* (Baird and Girard). Am. Midl. Nat. 65, 446–458.
Carton, A.G., Montgomery, J.C., 2004. A comparison of lateral line morphology of blue cod and torrentfish: two sandperches of the family Pinguipedidae. Environ. Biol. Fish. 70, 123–131.
Coombs, S., Montgomery, J.C., 1992. Fibers innervating different parts of the lateral line system of an Antarctic notothenioid, *Trematomus bernacchii*, have similar frequency responses, despite large variation in the peripheral morphology. Brain Behav. Evol. 40, 217–233.
Denton, E.J., Gray, J.A.B., 1988. Mechanical factors in the excitation of the lateral lines of fish. In: Atema, J., Fay, R.R., Popper, A.N., Tavolga, W.N. (Eds.), Sensory Biology of Aquatic Animals. Springer, New York, pp. 595–617.
Denton, E.J., Gray, J.A.B., 1989. Some observations on the forces acting on neuromasts in fish lateral line canals. In: Coombs, S., Gorner, P., Münz, H. (Eds.), The Mechanosensory Lateral Line: Neurobiology and Evolution. Springer, New York, pp. 229–246.
Dijkgraaf, S., 1963. The functioning and significance of the lateral-line organs. Biol. Rev. 38, 51–105.
Disler, N.N., Smirnov, S.A., 1977. Sensory organs of the lateral-line canal system in two percids and their importance in behavior. J. Fish. Res. Board Can. 34, 1492–1503.
Duponchelle, F., Ribbink, A.J., Msukwa, A., Mafuka, J., Mandere, D., Bootsma, H., 2005. Food partitioning within the species-rich benthic fish community of Lake Malawi, East Africa. Can. J. Fish. Aquat. Sci. 62, 1651–1664.
Fryer, G., 1959. The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. Proc. Zool. Soc. Lond. 132, 153–281.
Fryer, G., Iles, T.D., 1972. The Cichlid Fishes of the Great Lakes of Africa: Their Biology and Evolution. Oliver and Boyd, Edinburgh.
Genner, M.J., Turner, G.F., 2005. The mbuna cichlids of Lake Malawi: a model for rapid speciation and adaptive radiation. Fish Fish. 6, 1–34.
Genner, M.J., Turner, G.F., 2012. Ancient hybridization and phenotypic novelty within Lake Malawi's cichlid fish radiation. Mol. Biol. Evol. 29, 195–206.
Genner, M.J., Turner, G.F., Backer, S., Hawkins, S.J., 1999a. Niche segregation among Lake Malawi cichlid fishes? Evidence from stable isotope signatures. Ecol. Lett. 2, 185–190.
Genner, M.J., Turner, G.F., Hawkins, S.J., 1999b. Foraging of rocky habitat cichlid fishes in Lake Malawi: coexistence through niche partitioning? Oecologia 121, 283–292.
Goldschmidt, T., Witte, F., de Visser, J., 1990. Ecological segregation in zooplanktivorous haplochromine species (Pisces: Cichlidae) from Lake Victoria. Oikos 58, 343–355.
Hara, T., 1993. Role of olfaction in fish behavior. In: Pitcher, T.J. (Ed.), Behavior of Teleost Fishes. , 2nd ed. Chapman and Hall, London, pp. 171–200.
Hofmann, C.M., O'Quin, K.E., Marshall, N.J., Cronin, T.W., Seehausen, O., Carleton, K.L., 2009. The eyes have it: regulatory and structural changes both underlie cichlid visual pigment diversity. PLoS Biol. 7, e1000266, http://dx.doi.org/10.1371/journal.pbio.1000266.
Hori, M., Gashagaza, M.M., Nshombo, M., Kawanabe, H., 1993. Littoral fish communities in Lake Tanganyika: irreplaceable diversity supported by intricate interactions among species. Conserv. Biol. 7, 657–666.
Hulsey, C.D., Mims, M.C., Parnell, N.F., Streelman, J.T., 2010. Comparative rates of lower jaw diversification in cichlid adaptive radiations. J. Evol. Biol. 23, 1456–1467.
Janssen, J., 1997. Comparison of response distance to prey via the lateral line in the ruffe and yellow perch. J. Fish Biol. 51, 921–930.
Konings, A., 1990. Konings' Book of Cichlids and All the Other Fishes of Lake Malawi. TFH Publications Inc., Neptune City, NJ.

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Konings, A., 2007. Malawi Cichlids in Their Natural Habitat, 4th ed. Cichlid Press, El Paso, TX.
Liem, K.F., 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Syst. Biol. 22, 423–441.
Liem, K.F., 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. Am. Zool. 20, 295–314.
Martin, C.H., Genner, M.J., 2009. High niche overlap between two successfully coexisting pairs of Lake Malawi cichlid fishes. Can. J. Fish. Aquat. Sci. 66, 579–588.
McKay, K.R., Marsh, A., 1983. Food switching by two specialized algae-scraping cichlid fishes in Lake Malawi, Africa. Oecologia 56, 245–248.
Meuthen, D., Rick, I.P., Thünken, T., Baldauf, S.A., 2012. Visual prey detection by near-infrared cues in a fish. Naturwissenschaften 99, 1063–1066.
Miyazaki, T., Iwami, T., Meyer-Rochow, V.B., 2011. The position of the retinal area centralis changes with age in *Champsocephalus gunnari* (Channichthyidae), a predatory fish from coastal Antarctic waters. Polar Biol. 34, 1117–1123.
Mogdans, J., Nauroth, I.E., 2011. The oscar, *Astronotus ocellatus*, detects and discriminates dipole stimuli with the lateral line system. J. Comp. Phys. A 197, 959–968.
Montgomery, J.C., Coombs, S., Janssen, J., 1994. Form and function relationships in lateral line systems: comparative data from six species of Antarctic notothenioid fish. Brain Behav. Evol. 44, 299–306.
O'Brien, W.J., Evans, B.I., Browman, H.I., 1989. Flexible search tactics and efficient foraging in saltatory searching animals. Oecologica 80, 100–110.
O'Quin, K.E., Hofmann, C.M., Hofmann, H.A., Carleton, K.L., 2010. Parallel evolution of opsin gene expression in African cichlid fishes. Mol. Biol. Evol. 27, 2839–2854.
Ogle, D.H., Selgeby, J.H., Newman, R.M., Henry, M.G., 1995. Diet and feeding periodicity of ruffe in the St. Louis river estuary, Lake Superior. Trans. Am. Fish. Soc. 124, 356–369.
Parry, J.W.L., Carleton, K.L., Spady, T., Carboo, A., Hunt, D.M., Bowmaker, J.K., 2005. Mix and match color vision: tuning spectral sensitivity by differential opsin gene expression in Lake Malawi cichlids. Curr. Biol. 15, 1734–1739.
Peters, H.M., 1973. Anatomie und Entwicklungsgeschichte des Laterallissystems von *Tilapia* (Pisces, Cichlidae). Z. Morphol. Tiere 74, 89–161.
Rasband, W.S., 1997–2012. ImageJ. U.S. National Institutes of Health, Bethesda, MD, USA http://imagej.nih.gov/ij/
Reinthal, P.N., 1990. The feeding habits of a group of herbivorous rock-dwelling cichlid fishes (Cichlidae, Perciformes) from Lake Malawi, Africa. Environ. Biol. Fish. 27, 215–233.
Rezsu, E., Specziar, A., 2006. Ontogenetic diet profiles and size-dependent diet partitioning of ruffe *Gymnocephalus cernuus*, perch *Perca fluviatilis* and pumpkinseed *Lepomis gibbosus* in Lake Balaton. Ecol. Freshw. Fish 15, 339–349.
Schleuter, D., Eckmann, R., 2006. Competition between perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*): the advantage of turning night into day. Freshw. Biol. 51, 287–297.
Schleuter, D., Eckmann, R., 2008. Generalist versus specialist: the performances of perch and ruffe in a lake of low productivity. Ecol. Freshw. Fish 17, 86–99.
Schwalbe, M.A.B., Bassett, D.K., Webb, J.F., 2012. Feeding in the dark: lateral-line-mediated prey detection in the peacock cichlid *Aulonocara stuartgranti*. J. Exp. Biol. 215, 2060–2071.
Shcherbakov, D., Knörzer, A., Hilbig, R., Haas, U., Blum, M., 2012. Near-infrared orientation of Mozambique tilapia *Oreochromis mossambicus*. Zoology 115, 233–238.
Sivak, J.G., 1978. The functional significance of the aphakic space of the fish eye. Can. J. Zool. 56, 513–516.
Sturmbauer, C., Mark, W., Dallinger, R., 1992. Ecophysiology of Aufwuchs-eating cichlids in Lake Tanganyika: niche separation by trophic specialization. Environ. Biol. Fish. 35, 283–290.
Taplin, R.H., 2007. Experimental design and analysis to investigate predator preferences for prey. J. Exp. Mar. Biol. Ecol. 344, 116–122.
van Netten, S.M., 2006. Hydrodynamic detection by cupulae in a lateral line canal: functional relations between physics and physiology. Biol. Cybern. 94, 67–85.
Webb, J.F., 1989a. Gross morphology and evolution of the mechanosensory lateral line system in teleost fishes. Brain Behav. Evol. 33, 34–53.
Webb, J.F., 1989b. Neuromast morphology and lateral line trunk canal ontogeny in two species of cichlids: an SEM study. J. Morphol. 202, 53–68.
Webb, J.F., 2014. Morphological diversity, development, and evolution of the mechanosensory lateral line system. In: Coombs, S., Bleckmann, H., Fay, R., Popper, A.N. (Eds.), The Lateral Line System. Springer, New York, pp. 17–72.
Webb, J.F., Montgomery, J.C., Mogdans, J., 2008. Bioacoustics and the lateral line system of fishes. In: Webb, J.F., Fay, R.R., Popper, A.N. (Eds.), Fish Bioacoustics. Springer, New York, pp. 145–182.

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