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Ecological Limits on the Decoupling of Prey Capture and Processing in Fishes

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Synopsis Ray-finned fishes have two jaw systems, the oral and pharyngeal jaws, which perform functions associated with prey capture and processing, respectively. The structural independence of the jaw systems is recognized as having broad implications for the functional and ecological diversity of the radiation. Cichlids (and a few other lineages) possess a modified pharyngeal jaw system that enhances prey processing versatility and capacity. This innovation, pharyngognathy, is hypothesized to have freed the oral jaws to diversify in terms of prey capture. We test the relative role of prey capture properties (e.g., evasiveness) and prey processing (e.g., crushing) in driving divergent selection in the oral and pharyngeal jaws using a macroevolutionary model fitting framework. Evolutionary outcomes were asymmetric. All transitions between different properties of prey capture had a corresponding transition in properties of prey processing. In contrast, fewer than half the transitions in the properties of prey processing had a corresponding prey capture transition. This discrepancy was further highlighted by multi-peak models that reflect the opposing function of each jaw system, which fit better than null models for oral jaw traits, but not pharyngeal jaw traits. These results suggest that pharyngeal jaw function can change independently from the function of the oral jaws, but not vice versa. This finding highlights the possibility of ecological limits to the evolutionary decoupling of jaw systems. The independent actions of prey capture and processing may be decoupled, but their respective functional demands (and evolution) are not. Therefore, prey likely impose some degree of coordinated evolution between acquisition and processing functional morphology, even in decoupled jaw systems.

Introduction

The mechanisms underlying food acquisition and oral processing are highly diverse in vertebrates, including oral (Gans et al. 1978; Bemis and Lauder 1986; Bhullar et al. 2019), pharyngeal (Liem 1973; Wainwright et al. 2012), and tongue-biting systems (Sanford and Lauder 1989; Camp et al. 2009), with myriad modifications therein. Among such diversity, ray-finned fishes are exceptional for possessing two jaws systems (oral and pharyngeal) (Fig. 1). The structural independence of the oral and pharyngeal jaws is recognized as a major innovation with broad implications for the radiation (Liem 1973; Lauder 1982, 1983). Functional decoupling between the two jaws systems may permit the independent evolution of adaptations for prey capture and processing and thereby promote functional and ecological diversification (Liem 1973). Fish jaws are, correspondingly, a canonical example of functional decoupling (Lauder 1990; Farina et al. 2019). Subsequent modifications to the pharyngeal jaws, or pharyngognathy, in cichlids, labrids (wrasses and parrotfish), and others, is widely viewed as a major innovation underpinning much of those groups' trophic diversity (Liem 1973; Liem and Sanderson 1986; Wainwright et al. 2012; Wainwright and Longo 2017). Specifically, pharyngognathy enhanced the ability to generate bite force (Hulsey 2006; Hulsey et al. 2008) and increased the independent movement of the upper and lower pharyngeal jaws (UPJ and LPJ; Galis and Drucker 1996).

Despite the high profile of decoupled fish jaw systems and pharyngeal jaws as a major innovation, little is known about the macroevolutionary implications of these features. Functional decoupling is a mechanism that promotes diversification (Lauder 1990; Schaefer and Lauder 1996; Schkenk 2001) and functional innovations are predicted to be a major source of

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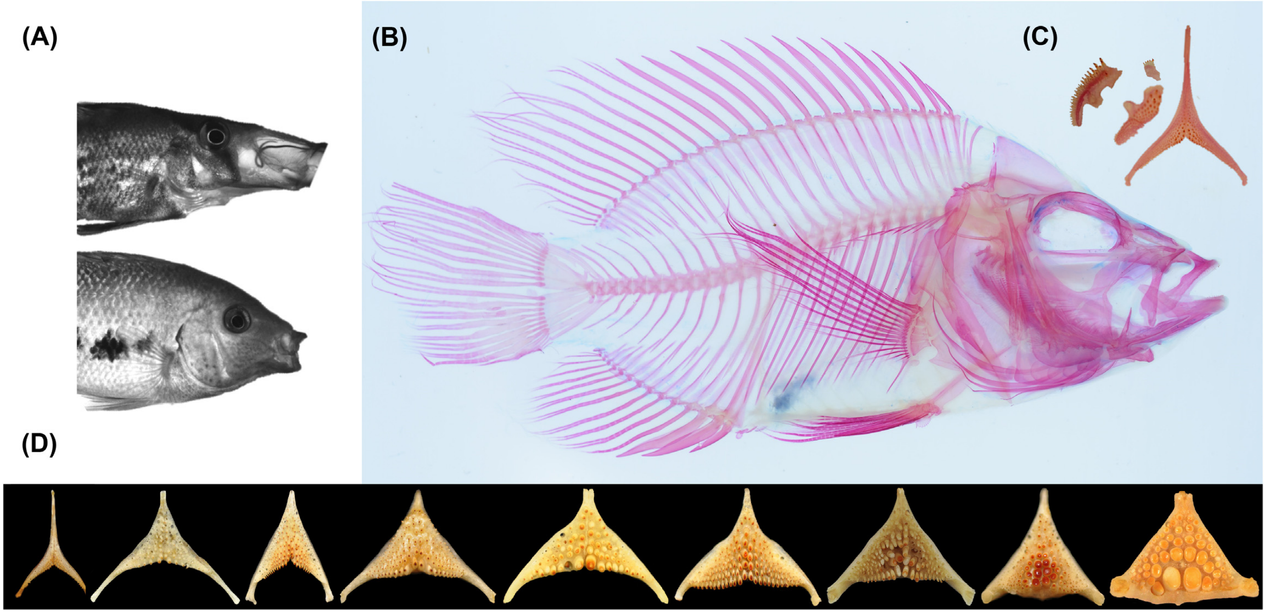

Fig. 1 Fish jaw systems. (**A**) Extreme protrusion of the oral jaws in *Caquetaia mysersi* (top) and modest protrusion of *Vieja fenestrata* (bottom) at maximum gape. (**B**) Cleared and stained *Chaetobranchus flavescens* (AUM49880) specimen revealing the anatomy of the oral jaw system. (**C**) The three main bone elements of the pharyngeal apparatus that engages with prey: lower pharyngeal jaw (i.e., the united fifth ceratobranchials), upper pharyngeal jaw (i.e., the united third and fourth pharyngobranchials), and the second pharyngobranchial. The upper pharyngeal jaw is shown in ventral and lateral view. (**D**) Representative diversity of the lower pharyngeal jaw in American cichlids. Oral and pharyngeal jaw structures measured in the study are labeled in Supplementary Fig. S1. Photos of *C. myersi* and *V. fenestrata* courtesy of Christopher Martinez. Photo of *C. flavescens* specimen courtesy of Alexus Roberts. All images of pharyngeal jaws by E.D.B.

ecological opportunity capable of driving adaptive radiation (Simpson 1953; Yoder et al. 2010; Stroud and Losos 2016). Within ray-finned fishes, labrids and cichlids are widely recognized for having modified pharyngeal jaws that enhanced their functional versatility, efficiency, and capacity (Liem 1973; Liem and Sanderson 1986; Galis and Drucker 1996; Mabuchi et al. 2007; Alfaro et al. 2009). Both of these radiations have reached bewildering diversity in terms of their feeding ecology and associated adaptations (Wainwright et al. 2004; Burress 2015; Burress and Wainwright 2019; Evans et al. 2019a; Larouche et al. 2020).

Functional morphology and kinematics of the oral jaws corresponds strongly to feeding ecology (Winemiller et al. 1995; Wainwright et al. 2001; Waltzek and Wainwright 2003; Hulsey et al. 2010; Price et al. 2011; Martinez et al. 2018; Evans et al. 2019b). However, functional morphology of the pharyngeal jaws also broadly reflects feeding ecology (Grubich 2003; Hulsey 2006; Hulsey et al. 2008; Burress 2016; Pos et al. 2019). Although jaw decoupling permits more functional versatility than a single jaw system, there remains some degree of correlated evolution between the oral and pharyngeal jaws (Hulsey et al. 2006a, ; Burress et al. 2020). Likewise, evolutionary integration among feeding structures might limit the independence of pharyngeal and oral jaw evolution (e.g., Watanabe et al. 2019; Evans et al. 2021). As such, the macroevolutionary signatures of functional decoupling on the jaw systems are unclear.

Pharyngeal jaws have mostly been recognized for their role in grinding algae (Xie 2001; Carr et al. 2006) and crushing mollusk shells (Wainwright 2005; Hulsey 2006; Hulsey et al. 2008). Although some fish crush mollusks with the oral jaws (e.g., tetraodontiforms and sheepshead; Palmer 1979; Norton 1988; Fernandez and Motta 1997; Friel and Wainwright 1999) or puncture shells with adaptations on the neurocranium (Norton 1988), most fishes do so with the pharyngeal jaws (Wainwright 2005). There is a large gradient in the capacity to generate bite force, reflected by relative enlargement of the pharyngeal jaw bones (Wainwright 2005; Burress 2016), elaboration of the interdigitating suture that unites the left and right LPJs (if present; Hulsey 2006), and the presence of robust molariform teeth along the posterior midline where structural stress is concentrated during mastication (Hulsey et al. 2008). Pharyngeal jaw movements also play a key role during winnowing—the process of separating edible items from a mouthful of inorganic items (i.e., sand; Drucker and Jensen 1991; Weller et al. 2017). Substrate sifting is a relatively widespread foraging strategy in cichlids (López-Fernández et al. 2013, 2014) and is associated with a specialized pharyngeal jaw morphology (Burress

2016). Zooplanktivory is also associated with a unique, highly atrophied pharyngeal jaw, whereas herbivores have expanded dentigerous surfaces packed with blade-like, serrated teeth (Casciotta and Arratia 1993; Burress 2016). Thus, pharyngeal jaws can be adapted to myriad processing demands imposed by prey items.

Liem (1973) hypothesized that these modified pharyngeal jaws freed the oral jaws from functional demands of prey processing and thereby allowed their diversification in terms of prey capture. Yet, the premise that diversification of the oral and pharyngeal jaw systems has principally been driven via divergent selection associated with prey capture and processing, respectively, has been more often implied than shown. The extent to which pharyngeal jaw functional morphology reflects fine-scale trophic patterns appears to also reflect functional morphology of the oral jaws (Casciotta and Arratia 1993; Burress 2016; Burress et al. 2020). There have been correspondingly few attempts to test predictions extending from Liem's decoupling hypothesis (but see Hulsey et al. 2008; Burress et al. 2020), despite its established place as canon in the fields of evolutionary morphology, functional morphology, and adaptive radiation (Kaufman and Liem 1982; Wainwright et al. 2012; Stroud and Losos 2016; Wainwright and Longo 2017; Farina et al. 2019). Here, we employ a macroevolutionary model fitting framework to test if the functional morphology of each jaw system is principally subject to divergent selection associated with their respective function (i.e., capture vs. processing) and, conversely, if each jaw system may be subject to residual selection associated with their alternative function. We used the clade of American cichlids as the focal group because of their ecological and morphological diversity (López-Fernández et al. 2012, 2013), and for the well-documented functional diversity of their oral and pharyngeal jaws (Casciotta and Arratia 1993; Hulsey 2006; Hulsey et al. 2006a, , 2008; Burress 2016; Burress et al. 2020).

Materials and methods

Functional morphology of the jaw systems

We used an existing dataset of functional morphological features of the oral and pharyngeal jaws for 84 species of Neotropical cichlid (Burress et al. 2020; Fig. 1; Supplementary Table S1). Oral jaw measurements included the dentigerous arm of the premaxilla, ascending process of the premaxilla, mandible, gape, protrusion, buccal cavity, closing and opening mechanical advantage of the lower jaw. These features have broad implications for feeding ecology, feeding performance, and prey capture (Wainwright and Richard 1995; Wainwright et al. 2001; Waltzek and Wainwright 2003; Hulsey et al. 2010). Pharyngeal jaw measurements included the aspect ratio of the LPJ, depth of the LPJ and UPJ, tooth diameter, size of the dentigerous surface of the LPJ, insertion of the primary muscle that operates the biting motion of the LPJ (i.e., fourth levator externus; LE4), and size of the facet on the UPJ that articulates against the neurocranium. These features have broad implications for feeding ecology and prey processing (Casciotta and Arratia 1993; Hulsey 2006; Hulsey et al. 2008; Burress 2016; Burress et al. 2016). Previous work has shown that different methods of size correction, log-shape ratios and phylogenetic residuals, have no effect on the outcomes of phylogenetic comparative analyses of American cichlids (Burress et al. 2020). Therefore, we accounted for size by converting measurements to log-shape ratios (Mosimann 1970) with the geometric mean of head size:

$$\log \text{trait}/(\text{head length} \times \text{head width} \times \text{head depth})^{1/3} \quad (1)$$

We chose this method over phylogenetic residuals for two reasons: (1) to avoid the assumption of Brownian motion (BM) and (2) because we felt that the geometric mean of head size was a more relevant metric of size for linear measurements that depict the size and shape of the jaws than body length (i.e., the normal reference dimension when calculating phylogenetic residuals).

Prey capture and processing selective regimes

We then defined two alternative selective regimes based on properties of prey capture and processing. Prey capture states consisted of evasive, semi-evasive, and non-evasive based on how prey evasiveness has been characterized in the literature (Martinez et al. 2018 and references therein; Supplementary Table S1). The evasive state included species that feed on prey capable of fast and sustained evasion (e.g., fishes, shrimps, crabs). The semi-evasive state included species that feed principally on organisms with a limited ability, either in duration or speed, to evade predators (e.g., aquatic insects). The non-evasive state includes species that feed on prey items that are attached to surfaces (e.g., algae or snails) or otherwise lack the ability to actively evade predators (e.g., plants and detritus). Prey processing states consisted of chew, grind, shear, grasp, and winnow, defined by the functional demands imposed by target prey, with some consideration of the architecture of pharyngeal dentition and frequency of different tooth types (Casciotta and Arratia 1993; Burress 2016). The chew state includes species that eat small soft-bodied items that only require light mastication by the pharyngeal jaws (e.g., most aquatic insects). This state represents the core function of the pharyngeal jaws, which to some extent, all pharyngeal jaws can perform. All other processes are more specialized along some functional dimension. The grind state includes species that feed on items that require prolonged processing, either to physically crush shelled organisms (e.g., mollusks) or rupture cells that would otherwise inhibit digestion (e.g., algae). The shear state included species that consume large fractions of living plant matter. The grasp state included species that principally feed on organisms consumed whole and merely need to be transported to the esophagus by the pharyngeal jaws (e.g., fishes). The winnow state included species that feed by plunging their mouths into the substrate to extract buried prey that is then separated from inedible items in the mouth (e.g., small aquatic insects and worms). When possible, these classifications were made in reference to detailed stomach content analyses (i.e., Burress 2016, and references therein). When such studies were not available, the classifications were inferred based on data from close relatives (i.e., congeners), from detailed inspections of anatomy (i.e., Casciotta and Arriata 1993), or from motion capture analyses of feeding (i.e., Wainwright et al. 2001; Waltzek and Wainwright 2003).

Phylogenetic comparative methods

For phylogenetic comparative analyses, we used an existing phylogeny of Burress and Tan (2017), later updated by Burress et al. (2019) to reflect the changing understanding of cichlid divergence (i.e., Matschiner et al. 2017). To determine if features of prey capture and optima drove divergent selection in jaw morphology, we employed a macroevolutionary model fitting framework. We specified *a priori* selective regimes for prey capture and processing as detailed above. We fitted four models of trait evolution using the OUwie function employed in the OUwie R package (Beaulieu et al. 2012; Beaulieu and O'Meara 2015). We estimated the evolutionary histories of the discrete characters using stochastic character mapping (Huelsenbeck et al. 2003) with the make.simmap function implemented in the PHYTOOLS package (Revell 2012). During this procedure, we allowed all transitions to have different rates (i.e., the all-rates-different model transition model; ARD), which was preferred over an equal rates model based on a modified Akaike information criterion (AIC_c) that incorporates a correction for small sample size (Burnham and Anderson 2002; Burnham et al. 2011). We also cross referenced the locations (i.e., nodes) of transitions in properties of prey capture and processing. We then assessed the proportion of coincident changes across the phylogeny (i.e., if a change in prey capture had a corresponding change in prey processing and vice versa). Since there is a discrepancy in the number of character states (three prey capture states and five prey processing states), we compared the observed proportion of coincident transitions with that of characters simulated under a BM process. We simulated 100 sets of two discrete characters, with three and five states, to match the observed characters. Discrete character histories were simulated using the rTraitDisc function implemented in ape (Paradis and Schliep 2019). We then estimated the evolutionary history of the simulated characters as described for the observed characters. This procedure resulted in a null distribution of expected coincident changes in character states that might arise from BM given the asymmetry of the observed character states.

We then fitted alternative evolutionary models. Fitted models included two null models: (1) a single-rate BM model that permits a single regime and trait evolution that proceeds as a random walk and trait variance that accumulated proportional to time (Felsenstein 1985) and (2) a single-optimum Ornstein-Uhlenbeck (OU1) model that constrains trait evolution toward a single value (θ) and allows a single α and σ^2 across all selective regimes. We then fitted two alternative multi-peak OU models that permit different θ and a single α and σ^2 across all selective regimes, one with selective regimes defined by the properties of prey capture and the other by properties of prey processing. The fits of these models were evaluated using AIC_c (Burnham and Anderson 2002; Burnham et al. 2011). To account for uncertainty in phylogenetic relationships and divergence times, we repeated these analyses across 100 trees randomly sampled from the posterior distribution. To ensure that we could properly distinguish among these models, we simulated data under BM, OU1, and OUM processes using the OUwie.sim function and then fitted each model to the simulated datasets (Supplementary Table S2).

Results

The inferred ancestral property of prey capture was non-evasive, with seven transitions, on average, to evasive prey and nine transitions, on average, to semi-evasive prey (Fig. 2). The inferred ancestral property of prey processing was crushing; with three transitions, on average, to winnowing; 12 transitions, on average, to chewing; six transitions, on average, to grasping; and one transition to shearing (Fig. 2). Every transition in prey capture had a corresponding transition in prey processing, whereas fewer than half of the prey processing transitions had a coincident prey capture transition (Supplementary Fig. S2). Both prey capture and processing were more likely to have a coincident transition in the opposing function than would be expected by a BM process (Supplementary Fig. S2). Oral jaw traits tended to be best-fit by the multi-peak OU model defined by properties of prey capture (Table 1). The ascending process of the premaxilla, jaw protrusion, and

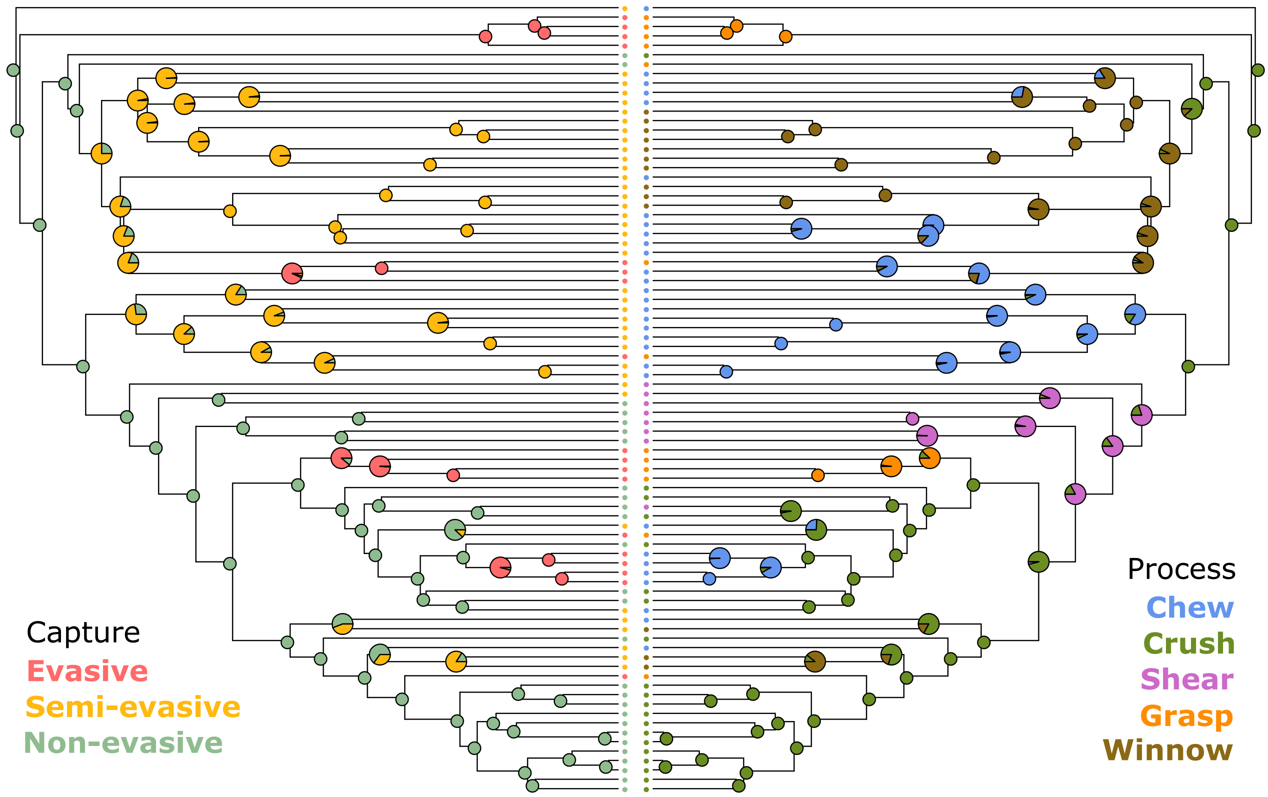

Fig. 2 Selective regimes associated with properties of prey capture and prey processing in American cichlids. Pies depict the probability of each state at each node. Dots along the tips of the phylogeny depict the character states of each species. The evolutionary histories were estimated with stochastic character mapping.

Table 1 Macroevolutionary models fit to oral and pharyngeal jaw traits

Trait	Best model	Comp. model	ΔAIC_c	Prop.	$F_{alt} > F_{null}$
Premaxilla	$OUM_{capture}$	—	16.1	0.90	Yes
Ascending process	$OUM_{capture}$	$OUM_{process}$	19.0	0.42	Yes
Mandible	$OUM_{capture}$	—	30.6	0.99	Yes
Gape	$OUM_{capture}$	—	15.4	0.98	Yes
Protrusion	$OUM_{capture}$	$OUM_{process}$	5.1	0.93	Yes
Buccal cavity	$OUM_{process}$	$OUM_{capture}$	4.9	0.21	Yes
MA_{close}	$OUM_{capture}$	—	8.0	1.00	Yes
MA_{open}	$OUM_{capture}$	—	24.3	1.00	Yes
LPJ aspect ratio	$OUM_{process}$	—	15.7	0.97	No
LPJ depth	$OUM_{process}$	—	11.8	0.68	No
UPJ depth	$OUM_{process}$	—	5.7	0.66	No
LPJ tooth size	$OUM_{process}$	—	5.6	1.00	No
LPJ dentigerous surface	$OUM_{process}$	—	10.1	0.94	No
LE4 insertion	$OUM_{capture}$	$OUM_{process}$	1.4	0.95	Yes
UPJ facet	$OUM_{process}$	$OUM_{capture}$	2.5	0.89	No

Note: Comparable models (Comp. model), difference in AIC_c values relative to the next best-fitting model across the MCC tree (ΔAIC_c), proportion of trees in which the overall best model was recovered as the best fitting model (Prop.), and if the OUM model associated with the opposing function (e.g., prey processing for oral jaw traits and prey capture for pharyngeal jaw traits) was better fit than null models (i.e., BM1 and OU1; $F_{alt} > F_{null}$). Comparable model includes alternative models within 5 ΔAIC_c or models in which the best fitting model was unresolved while accounting for phylogenetic uncertainty (i.e., cases in which Prop. was low).

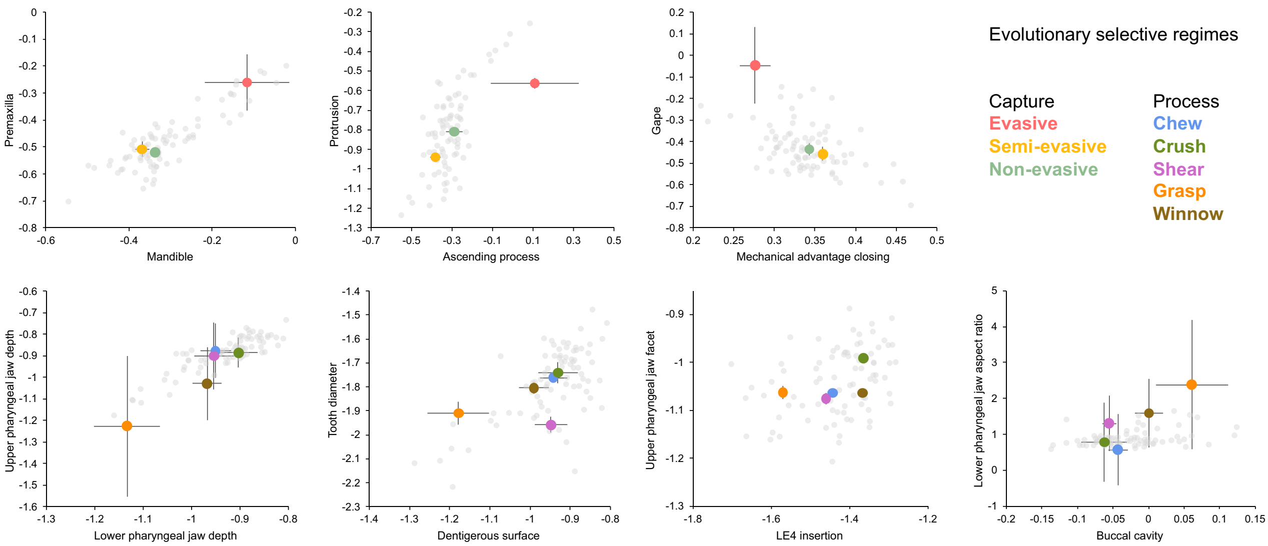

Fig. 3 The adaptive landscape defined by properties of prey capture and processing. Colors depict estimated evolutionary optima (mean ± 95% C.I.) for each character state. Gray dots depict species means. Note that optima were estimated separately for each trait, not in conjunction with the trait with which they are plotted.

size of the buccal cavity similarly fit multi-peak OU models defined by prey capture and processing (Table 1; Supplementary Table S3). Evasive prey had distinct optima for all oral jaw traits, whereas optima associated with semi-evasive and non-evasive prey were similar (Fig. 3). Pharyngeal jaws tended to be best-fit by multi-peak OU models defined by properties of prey processing (Table 1). The insertion of the muscular sling on the LPJ and size of the facet of articulation on the UPJ similarly fit multi-peak models defined by prey processing and capture (Table 1; Supplementary Table S3). Crushing, grasping, and winnowing tended to have distinct optima for most pharyngeal jaw traits (Fig. 3). Shearing had distinct optima for tooth diameter (Fig. 3). When considering the relative fit of multi-peak OU models defined by each jaw systems opposing function, the properties of prey processing comprehensively better fit oral jaw functional morphology than did null evolutionary models (Table 1). In contrast, properties of prey capture did not better fit pharyngeal jaw traits than did null evolutionary models (Table 1). Each model best fit data simulated under the corresponding model (Supplementary Table S2).

Discussion

Decoupling of prey capture and processing

Functional decoupling is a mechanism that promotes diversification by allowing independent specialization among anatomical features (Schaefer and Lauder 1996; Lauder 1990; Schwenk 2001). The partitioning of functional tasks associated with prey capture and processing between the oral and pharyngeal jaws, respectively, is a canonical example of such decoupling (Lauder 1990; Wainwright 2007; Farina et al. 2019), and has been invoked as a catalyst of adaptive radiation (Liem 1973; Kaufman and Liem 1982; Galis and Drucker 1996).

We found that the oral jaw functional morphology of American cichlids was principally subject to divergent selection associated with properties of prey capture (Table 1; Fig. 3). Oral jaws used to capture evasive prey tended to be large, highly protrusible, and characterized by relatively low mechanical advantage (Fig. 3). These adaptations reflect the need to generate suction, consume large prey, and produce rapid feeding strikes (Wainwright and Richard 1995; Bellwood et al. 2015). There are relatively large confidence intervals around the evasive optima (Fig. 3), likely reflecting functional diversity within that category. A major axis of variation associated with feeding on evasive prey is the relative use of suction versus ram (Liem 1978; Longo et al. 2016). Both foraging strategies are well-represented in American cichlids, with elongate predators that utilize high ram velocity (e.g., *Crenicichla*) and others that utilize extreme jaw protrusion to generate suction (e.g., *Petenia* and *Caquetaia*; Wainwright et al. 2001; Waltzek and Wainwright 2003; Hulsey et al. 2010). The high degree of variance around evasive prey optima may also reflect that some species decouple oral and pharyngeal jaws such that they have exceptional trophic flexibility (e.g., *Caquetaia* and *Crenicichla*, which consume both evasive and processing intensive prey), whereas others co-modify the two jaw systems to the extent that they are highly specialized piscivores (e.g., *Cichla* and *Petenia*; Burress et al. 2020). Oral jaws used to capture semi-evasive and non-evasive prey tended to have similar optima (Fig. 3), but there is considerable diversity not captured by our approach. For example, within the non-evasive category there are a variety of feeding ecologies that employ biting, picking, and suction (Winemiller et al. 1995). Although the oral jaws were principally subject to divergent selection associated with properties of prey *capture*, it is noteworthy that the multi-peak model (defined by prey *processing* properties) fitted all oral jaw traits better than did the null models (Supplementary Table S2).

Pharyngeal jaw functional morphology was principally subject to divergent selection associated with properties of prey processing (Table 1). Pharyngeal jaws merely used for grasping (i.e., prey consumed whole) tended to be shallow, with small teeth on a reduced dentigerous surface, reduced musculature, and a high aspect ratio LPJ (Fig. 3). These characteristics are consistent with a general atrophy of the pharyngeal jaw system, likely in response to constraints imposed by gape limitation (McGee et al. 2015; Burress et al. 2016; Burress and Wainwright 2020). Pharyngeal jaws used for crushing, either algae cells or mollusk shells, tended to be deep, with large teeth situated on an expanded dentigerous surface, well-developed musculature, and a low aspect ratio LPJ (Fig. 3). These adaptations are consistent with generating a strong bite and resisting the associated structural stress incurred during mastication (Hulsey 2006; Hulsey et al. 2008). Pharyngeal jaws used to shear living plant tissue tended to have small teeth that were laterally compressed into blade-like structures, situated on an expanded dentigerous surface, with a somewhat high aspect ratio (Fig. 3). These characteristics likely reflect a processing strategy tied to engaging prey with specialized dentition rather than the generation of a powerful bite (Casciotta and Arratia 1993; Burress 2016). Pharyngeal jaws used for winnowing edible items from inorganic material tended to be shallow, with a reduced dentigerous surface, well-developed musculature, and a high aspect ratio (Fig. 3). This combination of adaptations likely reflects the prolonged use of rapid movements during winnowing (Drucker and Jensen 1991; Weller et al. 2017), as opposed to the generation of a strong bite. Winnowing species also had a large buccal cavity (Fig. 3); however, this morphology may be associated with mouth brooding rather than winnowing, as the two traits are partly confounded by their co-occurrence in many South American cichlid species (Goodwin et al. 1998; López-Fernández et al. 2014).

Ecological limits on decoupled jaw systems

Prey have ecological, anatomical, and life history characteristics that establish the functional demands for would-be predators associated with both capture and processing. Because these are shared qualities of prey, the functional demands of prey capture and processing are correlated among different phases of prey interaction. This ecological non-independence forces the evolution of the oral and pharyngeal jaw systems to be coordinated to some minimum degree. In other words, there are some capture and processing adaptations that are incompatible. The clearest example of this phenomenon is with piscivory, especially in pharyngognathous fishes. Feeding on evasive prey requires the generation of sufficient suction force to draw prey into the mouth and, therefore, is associated with large protrusible oral jaws (Wainwright et al. 2001; Bellwood et al. 2015). In contrast, the pharyngeal jaws become largely inhibitory as fishes are consumed whole and require no complex functions by the pharyngeal jaws. Any small benefit of grasping and aiding in transporting prey to the esophagus is easily offset by the reduced gape imposed by pharyngognathy, which significantly reduces feeding efficiency and capacity (McGee et al. 2015; Burress and Wainwright 2020). Thus, predatory cichlids (and other pharyngognathous fishes) have the conundrum of possessing a burdensome toolset they do not need. Correspondingly, transitions to piscivory are relatively scant in these groups (Price et al. 2011; McGee et al. 2020). The shape of the pharyngeal jaw, especially its depth, is a strong predictor of piscivory in cichlids (Hellig et al. 2010; Burress 2016), as gracile bones relax gape limitations (Burress et al. 2016). One lineage has partially reversed pharyngognathy to further circumvent gape constraints (Burress and Wainwright 2020). Therefore, any feeding ecology that requires a robust pharyngeal jaw, such as powerful jaws for crushing mollusk shells (Hulsey 2006; Burress et al. 2016), is going to be at odds with the management of gape limitation.

Some aspects of prey capture and processing fundamentally trade-off with one another in ways that extend to decoupled jaw systems. Successful consumption of a prey item means the predator has suitably (or minimally) dealt with demands of prey capture and processing. The ecological non-independence of these functional demands may explain why there remains some degree of correlated evolution between the oral and pharyngeal jaws, despite considerable relaxation of constraints that would otherwise inhibit diversification of a single jaw system (Burress et al. 2020). Liem (1973) hypothesized that by taking on the demands of prey processing, pharyngeal jaws permitted the oral jaws to diversify in terms of prey capture. In many ways, this hypothesis has been corroborated by subsequent studies. The pharyngeal jaws play a central role in prey processing, performing functions impossible for the oral jaws alone (Hulsey 2006; Hulsey et al. 2006a,). There is a relaxed degree of integration between the jaw systems that promotes the trophic versatility and capacity (Hulsey et al. 2008; Burress et al. 2020). However, we highlight that the pharyngeal jaws are clearly the more unencumbered jaw system, being unconstrained by demands of prey capture, whereas the oral jaws remain subject to some degree of selection associated with prey processing. This result makes sense in light of the temporal sequence of prey capture followed by processing, but indicates a practical limit to functional decoupling imposed by the shared capture and processing qualities of prey.

Conclusions

Decoupled jaw systems promote diversity by permitting expanded combinations of functions that would not be possible with a single jaw system (Liem 1973; Lauder 1982, 1983; Burress et al. 2020). We show that even with decoupled jaws, the oral jaws may be subject to divergent selection associated with prey processing, pointing to ecological limits of functional decoupling. We further show that the extent of decoupling is strongly directional such that functions performed by the oral jaws diversify in unison with functions performed by the pharyngeal jaws, but that pharyngeal jaw functions can diversify independently. Consequently, pharyngeal jaws may not have promoted the diversification of the oral jaws in response to complete decoupling (i.e., Liem 1973), but rather enhanced the multifunctionality of oral jaw phenotypes in the face of limited decoupling. Ecological limits on the decoupling of anatomical systems may have implications for related processes like integration and modularity such that there may be similar limits to integration and the independence of modules within multifunctional biomechanical systems. Integration, while historically considered a constraint on evolution (Bookstein et al. 2003; Marroig et al. 2009), may also promote evolution by synchronizing responses to selective pressures (Watanabe et al. 2019; Evans et al. 2021), providing a pathway for rapid mechanical adaptation (Muñoz 2019). In contrast, modularity enables diversification by permitting a multitude of responses by different traits (or sets of traits) (Wagner 1996; Larouche et al. 2018). Carl Gans was fascinated by the anatomy and functional morphology of the feeding mechanism (Gans 1961; Gans et al. 1978, 1982), but was quick to question basic assumptions about their broader consequences (Gans 1969). In the spirit of the Gans award, we used this critical lens as motivation to ask fundamental questions about Liem's decoupling hypothesis, a canonical example of key innovation in the field of evolutionary biology.

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Supplementary data

Supplementary data available at *ICB* online.

Data availability

No new data were generated or analyzed in support of this research.

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