Biomechanical trade-offs bias rates of evolution in the feeding apparatus of fishes

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Morphological diversification does not proceed evenly across the organism. Some body parts tend to evolve at higher rates than others, and these rate biases are often attributed to sexual and natural selection or to genetic constraints. We hypothesized that variation in the rates of morphological evolution among body parts could also be related to the performance consequences of the functional systems that make up the body. Specifically, we tested the widely held expectation that the rate of evolution for a trait is negatively correlated with the strength of biomechanical trade-offs to which it is exposed. We quantified the magnitude of trade-offs acting on the morphological components of three feeding-related functional systems in four radiations of teleost fishes. After accounting for differences in the rates of morphological evolution between radiations, we found that traits that contribute more to performance trade-offs tend to evolve more rapidly, contrary to the prediction. While ecological and genetic factors are known to have strong effects on rates of phenotypic evolution, this study highlights the role of the biomechanical architecture of functional systems in biasing the rates and direction of trait evolution.

Keywords: functional morphology; performance; suction feeding; morphological diversification

1. INTRODUCTION

Trade-offs are often considered an impediment to adaptive evolution, potentially limiting the range of trait values and their rate of evolution [1–5]. Performance trade-offs stem from competing demands on a single trait (morphological, physiological or functional) that has strong effects on multiple aspects of performance. When a trait is associated with a trade-off, a change in the trait's value increases one aspect of performance, but simultaneously decreases other performance traits. It could therefore be expected that traits experiencing strong trade-offs (and therefore competing selective pressures) will evolve more slowly and show less variance, as they are under more constraints than those involved in weaker trade-offs.

An analogy can be drawn between this prediction and the effects of pleiotropy (a property of genes that affect multiple phenotypic traits) on rates of molecular evolution. Otto [6] stated that pleiotropic genes are slower to adapt and the phenotypic traits to which they contribute are limited in their responses to selection. Similarly, Carroll [7] concluded that 'mutations with greater pleiotropic effects will have more deleterious effects on organismal fitness and will be a less common source of variation in form than mutations with less widespread effects'. A study within yeast showed a significant negative correlation between the number of biological processes in which a gene is involved and its rate of evolution [8]. In the same way that multiple phenotypic consequences can constrain the evolutionary rate of genes exhibiting pleiotropic expression, trade-offs could limit diversification of morphological traits that affect multiple performance traits.

Multi-functionality and performance trade-offs are pervasive in biomechanical and physiological systems. Although theoretical treatments have concluded that performance trade-offs can have a strong influence on the rates and directions of phenotypic evolution [5,9], demonstrating the importance of trade-offs during evolution has been difficult [1,2]. Biomechanical theory provides a useful way to test the performance consequences of morphological changes [4,10], as a functional system can be described in terms of its component morphological or physiological traits (henceforth referred to as morphophysiological or m-p traits, as defined by Walker [5]) and the resulting performance output (e.g. force, momentum and speed transmission). Selection on a functional system's m-p traits (the selection gradient [11]) can be decomposed into separate gradients for the selection on performance output and the m-p traits' effects on performance [12]. This framework has been extended to show that trade-offs between performance traits stem from the underlying m-p traits that affect performance traits in opposing ways [5,9]. These performance trade-offs can therefore be quantified as the negative relationship between performance traits arising from the overall effects of all underlying m-p traits.

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Not all the m-p elements of the functional system have the same contribution to the performance trade-off. To illustrate this, consider a functional system such as the jaw-closing mechanism of teleost fishes. A performance trade-off between closing force and jaw displacement (the movement of the jaw's tip per unit shortening of the muscle) is expected because the jaw acts as a lever. The lever mechanics of this system dictate that morphological changes that induce larger closing displacement will simultaneously transmit weaker closing force to the jaw [13]. When multiple m-p traits determine performance, however, not all traits necessarily contribute equally to the trade-off; some traits may have no effect, or perhaps even positive effects on other performance variables. Biomechanical theory [13,14] predicts that the closing force of the lower jaw in teleosts is primarily a function of the jaw's lever ratio (see equation (2.3) below) and the cross-sectional area of the lower jaw adductor muscles. Lower jaw-closing displacement is expected to be inversely related to this lever ratio, but unrelated to the cross-sectional area of the adductor muscles. Therefore, changes in the cross-sectional area of the closing muscle should not affect the closing displacement, whereas the lever ratio simultaneously influences both functions.

Walker [5] predicted that the contribution of an m-p trait to the trade-off between performance variables should be inversely proportional to the selection gradient acting on it. Walker [5] predicted that if an m-p trait has an effect on only one performance variable (and therefore no contribution to the trade-off), the selection gradient acting on it would be greater in magnitude than the selection gradient acting on an m-p trait that has opposite effects on the two performance variables. For example, in the lower jaw system, the cross-sectional area of the adductor muscle affects only the jaw-closing force, but closing in-lever affects both force and displacement, and overall selection is expected to operate more strongly on the former. Although the relationship between the magnitude of selection and rates of morphological evolution are not straightforward, different selection magnitudes may lead to biases in rates and directions of trait evolution [15,16], and rapid rates of morphological evolution are often taken as an indication of diversifying selection or adaptive radiation [17–20]. Although the model of Walker [5] can be used to quantify the contribution of m-p traits to the trade-offs between performance variables, empirical tests are required to evaluate the predicted inverse relationship between the contribution to trade-offs and rates of evolution.

Our goal in this study was to test the hypothesis that constraints imposed by the biomechanical architecture of functional systems bias the rate of evolution in the underlying components. Specifically, we asked whether traits that experience strong trade-offs evolve more slowly and show less variance among species than those involved in weaker trade-offs. We quantified the magnitude of performance trade-offs in three feeding-related functional systems in four radiations of teleost fishes and determined the effect of each m-p trait on the overall trade-off. We estimated the rates of evolution for m-p traits, and tested whether the estimated rates are correlated with the partial contribution of each trait to the performance trade-off.

2. METHODS

(a) *Functional systems*

We used data from the feeding apparatus of four teleost radiations to test the hypothesis that constraints imposed by the architecture of functional systems bias the rate of evolution of the system's components. We focused on three well-studied biomechanical systems: (i) the buccal expansion mechanism, (ii) the closing mechanism of the lower jaw and (iii) the opening mechanism of the lower jaw. These biomechanical systems are at least partly responsible for the success of prey capture in a wide variety of fish radiations [13,21–25].

The expansion of the buccal cavity is summarized by the suction index (SI; figure 1a–c), a performance metric that estimates maximal buccal pressure as a function of the transmission of force from the epaxial muscles (proportional to the cross-sectional area of that muscle) to elevate the cranium and expand the buccal cavity [22,26]. In brief, the SI incorporates measurements of five m-p traits (1, gape width; 2, buccal length; 3, cross-sectional area of the epaxial muscles; 4, the lengths of the in-lever; and 5, the length of the out-levers that transmit force and displacement from the epaxial muscles) to determine the morphological potential for suction production, following the equation

$$\text{SI} = \frac{\text{csaE} \times (L_{\text{in}}/L_{\text{out}})}{B_{\text{length}} \times \text{gape}}. \tag{2.1}$$

SI is suction index, L_{in} is the length of the moment arm for the epaxial muscles, L_{out} is the moment arm for the force owing to the buccal pressure drop, csaE is the cross-sectional area of the epaxial muscles and $B_{\text{length}} \times$ gape gives the projected area of the buccal cavity [22]. Functionally, SI can be used to predict the peak flow speed that a fish can produce at its mouth. Hydrodynamic principles (the Bernoulli principle [27,28]), as well as empirical measurements [26,29], indicate that squared peak flow speed is correlated with peak buccal pressure and with SI. Energetic considerations indicate a direct trade-off between suction pressure and another ecologically important aspect of feeding performance: volumetric expansion of the buccal cavity [21]. Buccal volume (BV) expansion can be approximated by the buccal area (B_{area}) and gape diameter such that

$$\text{BV} \cong B_{\text{area}} \times \text{gape}. \tag{2.2}$$

The ability of a suction-feeding predator to capture elusive prey is also limited by the speed and strength of mouth opening and closing (figure 1d–f), which are functions of the cranial muscles' capacities to generate force and velocity, and the lower jaw's ability to transfer force and velocity to mouth opening and closing [24]. The adductor mandibulae (AM) muscle actuates mouth closing by direct attachments to the lower jaw [30]. Movement is translated from the muscle to mouth closing through a simple lever system. Thus, the closing force of the lower jaw can be approximated by

$$F_{\text{close}} = \text{csaAM} \times \frac{L_{\text{in}}}{L_{\text{out}}}, \tag{2.3}$$

where F_{close} (the closing force) is determined by the following three m-p traits: csaAM, the cross-sectional area of the adductor mandibulae muscle; L_{in}, the length of the moment arm for the AM muscle; and L_{out}, the moment arm for the force owing to the closing jaw. The mechanical advantage, which is defined as the ratio of in-lever to out-lever, reflects a trade-off between transmission of force and movement to the anterior tip of the lower jaw (D_{tip}). Under this trade-off, larger values of
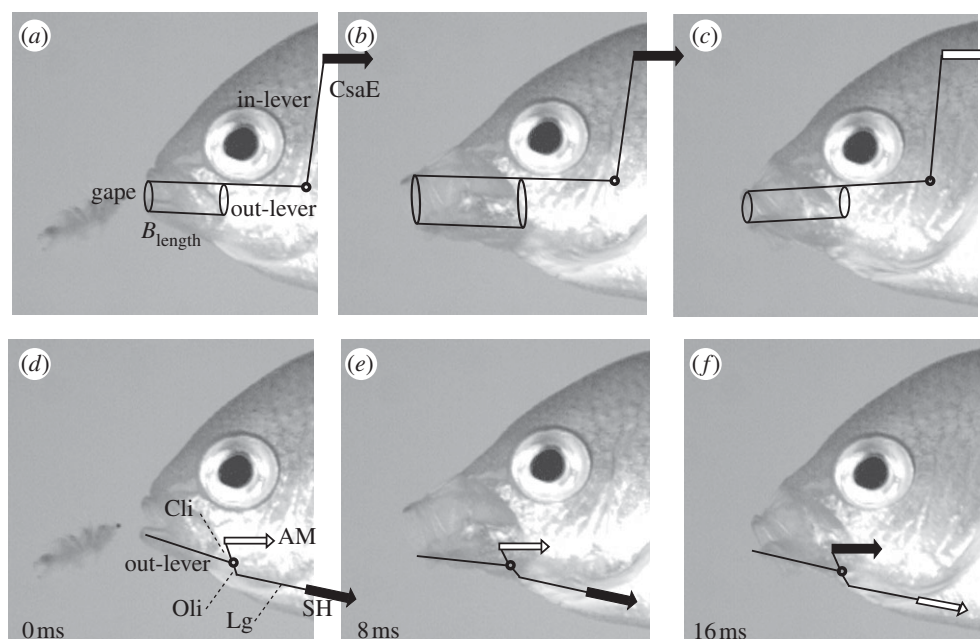
Figure 1. Trade-offs in suction-feeding performance in Acanthomorph fishes. The suction index (*a–c*) represents the transmission of force from the epaxial muscle through a lever system to expand the buccal cavity (expanding cylinder in (*a–b*)) and generate a flow of water carries the prey towards the fish. Buccal expansion is accompanied by the opening of the lower jaw through contraction of the sternohyoid muscle SH; (*d–f*). That muscle is connected to the opening in-lever of the jaw through a series of ligaments (see the electronic supplementary material for details). To keep live prey within the mouth, the adductor mandibulae (AM) muscle contracts, transmitting force through a lever system (*d–f*) to rapidly close the mouth. Illustration is based on a 20 ms sequence of *Chromis viridis* feeding on an *Artemia* sp., originally filmed at 500 frames per second. Muscle-contraction phase is denoted by black arrows representing the AM, SH and epaxial muscles. Cli, closing in-lever; Oli, opening in-lever; Lg, ligament system connecting the lower jaw to the SH; B_{length}, buccal length; CsaE, cross-sectional area of the epaxial.

mechanical advantage will transmit more force per unit input force, whereas smaller ratios tend to amplify input displacement, as given by

$$D_{tip} \cong \frac{L_{out}}{L_{in}}. \qquad (2.4)$$

To the best of our judgement, SI is not a good descriptor of the capacity of labrids to generate negative pressure in the mouth cavity. We therefore used part of the jaw-opening mechanism as a second functional system in this radiation. The opening of the mouth in labrids is largely powered through the contraction of the sternohyoideus muscle, which acts as the major jaw depressor [31], transmitting its force through the interopercular-mandibular ligament to the in- and out-lever of the jaw (see details in the electronic supplementary material). The transmission of force and displacement was calculated in a way similar to the jaw-closing mechanism (equations (2.3) and (2.4); figure 1*d–f*). While there are other linkages that can contribute to jaw depression in all of the fish groups we studied, all of these systems depress the mandible by transmitting force and displacement through the above mechanism. See the electronic supplementary material for details on measurements of each of the morphological variables.

(b) *Estimating performance trade-offs*
We build on a model of functional constraints on performance evolution [5,32] to evaluate the consequences of performance trade-offs for the evolution of m-p and performance traits [33]. We used partial residuals to estimate the contribution to the trade-off for each of the five traits that affect the buccal expansion and for each of the three traits

that affect jaw closing and opening (figure 1; see electronic supplementary material). Strong trade-offs occur when the correlation between partial residuals for an m-p trait is large in magnitude and negative, indicating that the trait has opposite effects on the performance variables. Facilitation can also occur when the correlation is large and positive, indicating that the m-p trait affects both performances in the same direction. Finally, we define lack of trade-off as the state when the correlation coefficient is not different from 0, indicating that the m-p trait has very small or no effect on one of the performance variables.

(c) *Comparative analysis*
We used phylogenetic independent contrasts (see the electronic supplementary material for details on statistical analysis using contrasts) to account for covariance between species values owing to phylogeny [34,35]. Trait values were log-transformed and size-corrected following the study of Revell [36]. We used species-level, time-calibrated molecular phylogenies as the basis for calculating contrasts (electronic supplementary material, table S1). The four phylogenies differ in the number and nature of the genes used and in the methods used to reconstruct tree topology and date divergence times. However, if an effect is found despite the methodological differences in reconstructing phylogenies, we believe it would suggest our analyses are robust to such differences.

3. RESULTS
(a) *Performance trade-offs*
We found strong, significant performance trade-offs ($p < 0.028$; electronic supplementary material, table S2) between the buccal expansion performance traits SI
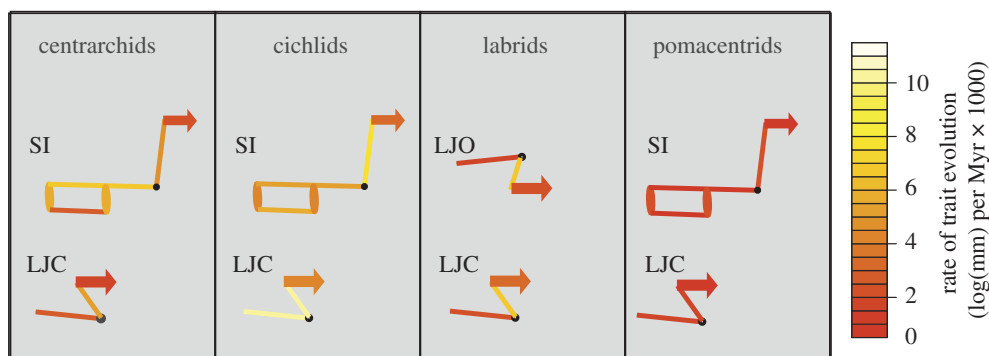
Figure 2. Rates of trait evolution in three functional systems as estimated in four radiations of teleost fishes. Functional systems measured included the lower jaw-closing mechanism (LJC), lower jaw-opening mechanism (LJO) and the components of the buccal expansion mechanism (SI). Rates of trait evolution were estimated based on a model of Brownian motion evolution, and are in units of log(mm) per million years. See figure 1 for details on each system's components.

Table 1. ANCOVA Summary table for the effect of radiation and contribution to performance trade-off on rates of morphological evolution. Statistics for the overall model: Adj $r^2 = 0.45$, $F_{4,25} = 7.043$, $p < 0.001$. The interaction between slope and radiation was non-significant ($p > 0.39$; electronic supplementary material, table S3).

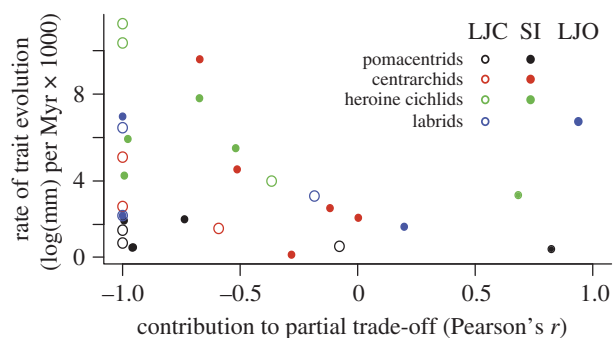| effect	estimate	iterations	probability
contribution to trade-off	-1.80×10^{-4}	3222	0.028
clade (Pomacentridae)	-2.52×10^{-4}	4366	0.02
clade (Centrarchidae)	-4.79×10^{-6}	292	0.26
clade (Cichlidae)	2.66×10^{-4}	5000	0.001

Figure 3. Correspondence between a trait's effect on a performance trade-off and its rate of evolution. The effect of each trait on the trade-off was quantified as the Pearson's correlation, r, between the partial residuals of two performance traits. The rate of trait evolution is the estimated rate parameter for a Brownian model of evolution and is reported in units of log(mm) per millions of years. Open symbols represent values for the components of the lower jaw-closing mechanism (LJC; abductor muscle, in-lever, out-lever), closed symbols represent values for the buccal expansion mechanism (SI; gape, buccal length, CsaE, in-lever, out-lever) or lower jaw-opening mechanism in labrids (LJO; muscle, in-lever, out-lever).

and BV. We also found significant performance trade-offs between the jaw-opening and -closing performance traits force and displacement ($p < 0.034$; electronic supplementary material, table S2). Correlations between performance variables for the buccal expansion system (between SI and BV) ranged from $r = -0.73$ to -0.42, and those for the lower jaw system (between force and displacement) ranged from $r = -0.78$ to -0.55 (electronic supplementary material, table S2). The magnitudes of performance trade-offs were not significantly correlated with the rates of evolution in SI, BV, jaw displacement or jaw force ($p > 0.05$ in all cases). Electronic supplementary material, table S4 details contribution of each trait to the performance trade-offs.

(b) *Rates of morphological evolution*
We found considerable variation between fish groups in the rate of morphological evolution of system components (permutation-based ANCOVA, $p < 0.014$; table 1). Cichlids had the highest rates (6.56×10^{-4} mm Myr^{-1}), while pomacentrids had the lowest overall rates (1.38×10^{-4} mm Myr^{-1}; figure 2 and table 1). There was no effect of the functional system (buccal expansion and lower jaw) on the magnitude of those rates, and the interaction between functional system and radiation was non-significant (electronic supplementary material, table S3; $p > 0.24$ for system effect and $p > 0.39$ for the interaction).

(c) *Effects of trade-offs on rates of morphological evolution*
Across radiations, there was a significant effect of each trait's contribution to performance trade-offs on its rate of evolution (permutation-based ANCOVA, $r^2 = 0.53$, overall model $F_{4,25} = 7.04$, $p < 0.001$; trade-off effect, $p < 0.028$; figure 3 and table 1), such that stronger trade-offs were associated with faster rates of evolution. Radiation had a significant effect on the intercept (permutation-based ANCOVA, $p < 0.014$; table 1) but not on the slope of the regression. Models that included an interaction between contribution of the trade-off and functional system were not supported over the simpler models (electronic supplementary material, table S3; $p > 0.05$).

4. DISCUSSION
Trade-offs are often considered an impediment to adaptive evolution, potentially limiting the range of trait values and the rate of their evolution [5,9,32]. However, we found that elements of functional systems that are

subjected to stronger opposing functional demands display higher rates of evolution, contrary to our original prediction. The trend we observed implies a mechanism that could potentially explain variation in the rates of evolution on different body parts within clades. m-p traits that contribute little to a performance trade-off are unconstrained by opposing functional demands, and as long as selection gradients are similar on the different aspects of performance, they experience stronger selection than m-p traits facing more severe performance trade-offs. Stronger selection results in rapid evolution towards an adaptive peak [37], where selection maintains trait values within a limited range. The slower rate of evolution of m-p traits contributing little to performance trade-offs may therefore reflect selection resisting phenotypic divergence away from adaptive forms. In contrast, a single, steep adaptive peak might be less likely to exist for m-p traits that affect performance in opposite ways because extreme trait values may be beneficial for one aspect of performance but result in diminished performance along other axes. That is, the trade-off leads to a smaller net selection gradient acting on an m-p trait, flattening out the adaptive landscape and resulting in broader areas of phenotypic space corresponding to high fitness or many smaller, shallower peaks [38]. If the adaptive landscape is flatter, movement from one adaptive peak (or subpeak) to another might be easier, as intermediate steps may correspond to less reduction in fitness. Such a mechanism could ultimately translate to faster evolutionary rates for traits that contribute to performance trade-offs. However, other mechanisms (such as variable selection gradients for the different performance traits) cannot be ruled out. A thorough, theory-based mechanistic explanation for the effects of trade-offs on rates of morphological evolution is currently lacking, although it could potentially provide a mechanistic explanation for the observed patterns.

It is well documented that traits do not respond equally to selection, and understanding the mechanisms that underlie biases in rates and directions of phenotypic evolution is a major goal in evolutionary biology. Rate biases between body parts are often attributed to variation in selection pressure, when selection gradients affect specific functional systems [20,39]. Even in the presence of selection, genetic variance is necessary for traits to evolve, and so serves as a proxy for the immediate evolutionary potential of a trait. In many cases, traits evolve along genetic lines of least resistance, or as a response to other genetic constraints [40–43]. According to this mechanism, traits vary in their genetic potential to respond to selection, and constraints can bias the rates and directions of trait evolution. Similarly, genetic correlations can impose biases, and even link functionally unrelated traits and lead to trade-offs [44]. Much work has been done on characterizing and parametrizing the genetic covariance matrix (the **G** matrix) [40–43]. In much the same way as intrinsic genetic factors can influence the rates at which traits respond to selection, functional relationships between m-p traits and performance variables can bias phenotypic evolution. To our knowledge, our study is the first to test some theoretical predictions regarding the effects of performance trade-offs suggested by Walker [5].

We found significant differences in the rates of morphological evolution between the four clades tested (table 1). Cichlids, known for rapid lineage diversification

[45,46], displayed the fastest rate of the four clades. Interestingly, our dataset included only the heroine cichlids, which have much slower lineage diversification rates than African cichlids [45]. Pomacentrids had the slowest rates, followed by centrarchids and labrids. It could be that these rate differences are associated with the high diet diversity in cichlids and labrids [47,48] compared with pomacentrids [49], and particularly the lack of piscivores and hard-prey specialists in this latter radiation.

Our analysis of the rate of evolution in fish feeding traits clearly shows that diversification does not proceed at a constant rate across the trophic apparatus (figure 2). Different components of these biomechanical systems displayed rates that varied by an order of magnitude, and the fastest and slowest evolving traits differed between fish groups. Such rate biases are often attributed to sexual and natural selection, or to genetic constraints. However, our results suggest that biases in rates of morphological evolution between body parts can also be related to the architecture of the functional systems of which they are a part. While ecological and genetic factors are known to have strong effects on the rates of phenotypic evolution, this study highlights the role of biomechanical architecture in biasing rates and direction of trait evolution.

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