

Functional Complexity Can Mitigate Performance Trade-Offs

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ABSTRACT: Trade-offs are believed to impose major constraints on adaptive evolution, and they arise when modification of a trait improves one aspect of performance but incurs a cost in another. Here we show that performance costs that result from competing demands on one trait can be mitigated by compensatory changes in other traits, so long as performance has a complex basis. Numerical simulations indicate that increases in the number of traits that determine performance decrease the strength of performance trade-offs. In centrarchid fishes, multiple traits underlie suction feeding performance, and experimental data and hydrodynamic modeling show that combinations of traits evolve to increase the ability to feed on attached prey while mitigating costs to performance on evasive prey. Diet data for centrarchid species reveal a weak trade-off between these prey types, corroborating the results based on hydrodynamic modeling and suggesting that complexity in the functional basis of suction feeding performance enhances trophic diversification. Complexity may thus permit the evolution of combinations of high-performance behaviors that appear to violate underlying trade-offs, such as the ability to exert high suction forces with large gape. This phenomenon may promote morphological, functional, and ecological diversification in the face of the myriad selective demands organisms encounter.

Keywords: functional morphology, niche breadth, performance, suction feeding.

Introduction

Functional trade-offs are thought to place strong constraints on the evolution of organismal performance (Futuyma and Moreno 1988; Koehl 1996; Bennett and Lenski 2007; Wainwright 2007; Walker 2007). For example, changes in caudal fin area in fishes may have a positive effect on maximum escape speed and attractiveness to females but a negative effect on swimming endurance, and increases in fast-start speed may be limited by egg-carrying

capacity in females (Ghalambor et al. 2004). Similarly, changes in beak depth in finches confer enhanced ability to crush seeds but diminished performance in handling insect prey (Herrel et al. 2009). Thus, the evolution of a performance trait typically involves a balance between direct selection acting on it and correlated selection acting on other performance traits with which it trades off (Ghalambor et al. 2003; Walker 2007).

Functional trade-offs stem from competing demands on a single phenotypic (morphological, physiological, or functional) trait that has strong effects on multiple aspects of performance, such that a change in the trait's value increases one aspect of performance but simultaneously decreases one or more other performance traits. In the case of escape performance in guppies (Ghalambor et al. 2004), increases in body depth and mass enhance fast-start performance but lower egg-carrying capacity. Another example is jumping performance in *Anolis* lizards; increases in the ratio of lower to upper hindlimb lengths enhance jumping distance (Toro et al. 2004) but lower sprint speeds (Bauwens et al. 1995). Although performance trade-offs are considered pervasive in biological systems, demonstrating their importance during evolution has been difficult (Futuyma and Moreno 1988; Bennett and Lenski 2007). One possible explanation for this difficulty is that many functional systems are complex; that is, they are determined by multiple interacting component traits (Koehl 1996; Hulseley and Wainwright 2002; Alfaro et al. 2004, 2005; Toro et al. 2004; Collar and Wainwright 2006; Wainwright 2007). Identifying trade-offs may be especially challenging in complex systems because performance costs that result from competing demands on one trait are mitigated by independent, compensatory changes in other traits.

In this article we explore the potential for complexity to influence the evolution of organismal performance. Our primary thesis is that complex performance traits—those that are determined by multiple morphological or functional components—are less constrained during evolution

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by functional trade-offs than are simple performance traits—those determined by only a single underlying component. We test this hypothesis using suction feeding performance in fishes, a complex functional system determined by many interacting cranial elements.

Teleost fishes are characterized by a highly kinetic skull with multiple movable elements. During suction feeding, a predator rapidly opens its mouth and expands its buccal cavity through coordinated contraction of the epaxial and sternohyoideus muscles, resulting in elevation of the neurocranium, depression of the hyoid, abduction of the suspensoria, and downward rotation of the lower jaw (Osse 1969). The expansion of the buccal cavity generates a flow of water into the mouth and a spatial gradient of flow in front of it (Muller et al. 1982; Wainwright et al. 2007). This induced water flow exerts a force on the prey that is directed toward the mouth and counters forces generated by fleeing or attached prey (Holzman et al. 2007; Wainwright and Day 2007; Wainwright et al. 2007; Van Wassenbergh and Aerts 2009). The spatial reach of the induced flow is limited by gape size (Day et al. 2005; Wainwright and Day 2007; Wainwright et al. 2007) such that increasing the gape enables suction feeding fish to accelerate water and affect prey at a distance farther from the mouth. However, such increases in gape decrease the magnitude of hydrodynamic forces on prey via two separate mechanisms. First, increasing gape size results in a larger buccal cavity, and muscle power limitations dictate that increases in volumetric expansion lessen the capacity to produce suction pressure (Carroll et al. 2004; Carroll and Wainwright 2009). Second, increases in gape size reduce the spatial gradient of flow speed in front of the mouth and thus decrease the force due to the pressure gradient surrounding the prey, which is a major component of the hydrodynamic force exerted on the prey (Wainwright and Day 2007; Wainwright et al. 2007). Therefore, gape size is subject to the competing demands of generating large hydrodynamic forces and affecting prey that are farther in front of the mouth.

As long as fish use suction as their main prey capture strategy, this force-reach trade-off is expected to result in a conflict between the ability to feed on attached prey, such as some insect larvae and other benthic organisms, and evasive prey, such as fish and crayfish. Diets of fish species from a wide range of taxa suggest that the attached-evasive prey axis is important during trophic diversification, with many examples of specialization in these two groups (Schluter 1995; Huckins 1997; Westneat 2001; Wainwright and Bellwood 2002; Bellwood et al. 2006; Rice 2008). In the context of suction feeding, a fish's ability to feed on attached prey is determined by the force produced to dislodge the prey from the substrate to which it clings, while the success rate of feeding on evasive prey is likely

limited by the volume of water the fish can accelerate (Higham et al. 2006a; Carroll and Wainwright 2009; Collar et al. 2009). If the forces exerted on the prey were determined exclusively by the fish's ability to generate strong intraoral pressure, we would expect severe performance and dietary trade-offs. However, multiple factors contribute to a fish's capacity to produce this force (fig. 1): the magnitude of peak flow speed (Van Wassenbergh et al. 2006b; Holzman et al. 2007; Wainwright and Day 2007),

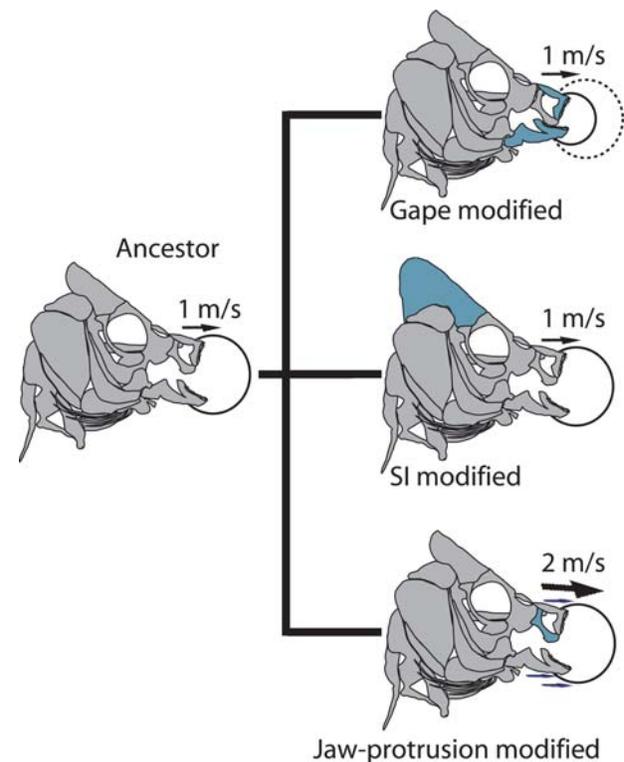


Figure 1: Three functional components may be modified during evolution to enhance the force a suction feeding fish exerts on its prey. Relative to an ancestor, increases in force capacity can be achieved through reduction in gape size (*top*), increased capacity to generate strong suction pressure (*middle*), or increased mouth displacement speed (*bottom*). Whereas reduction of gape decreases the spatial reach of the flow field (*solid and dashed circles in front of mouth*), force capacity may be modified without incurring this trade-off by increasing suction pressure capacity (expanded supraoccipital crest reflects larger area of muscle attachment, increased muscle force, and mechanical advantage for buccal expansion) or by increasing jaw protrusion speed (extended velocity vector above premaxilla). By modifying combinations of these components, it is possible for evolutionary increases in force to occur in the absence of steep costs to the spatial reach of the flow, which can weaken a potential trade-off between the ability to capture attached versus evasive prey. Shaded areas indicate areas that potentially evolve compared to ancestor, drawn based on *Lepomis macrochirus* morphology. *SI* = suction index.

speed of mouth displacement toward the prey (Holzman et al. 2008a, 2008b), and steepness of the gradient of flow speed, which is negatively correlated with the size of the mouth aperture (Wainwright and Day 2007; Wainwright et al. 2007). If these three components evolve independently, force on the prey may be increased through the evolution of combinations of components that minimize the cost to the reach of the suction flows. Conversely, evolutionary increases in gape to enhance feeding performance on large elusive prey need not result in a decrement to feeding performance on attached prey.

This study tests the hypothesis that functional complexity, defined here as a property of performance traits that are determined by multiple underlying traits, can mitigate performance trade-offs. To evaluate the general consequences of increasing complexity, we calculate performance trade-offs in simulated functional systems that vary in the number of performance-determining traits. We then investigate the effects of complexity in the suction feeding mechanism of centrarchid fishes using empirical data for strike kinematics, hydrodynamic modeling, and data for the contribution of attached and evasive prey to species' diets. We find a weak trade-off between evolutionary changes in the ability to feed on attached and evasive prey and show that the magnitude of the trade-off is much lower than would be expected if performance were determined by fewer traits.

Methods

Evaluating Performance Trade-Offs in Simulated Functional Systems

We used numerical simulations to explore the behavior of a hypothetical performance trade-off under increasing levels of functional complexity. To do this we built on a general framework for identifying functional constraints on the evolution of performance (Ghalambor et al. 2003; Walker 2007) and quantified the trade-off for varying levels of complexity, defined as the number of traits that determine performance. A more complete description of our framework is in appendix A in the online edition of the *American Naturalist* and is presented here only in brief.

Trade-offs between any two performance traits emerge as a consequence of the functional architecture of the system (Ghalambor et al. 2003; Walker 2007). The causal relationships between a set of morphological, functional, or physiological variables and the performance traits they determine can be described by a matrix \mathbf{F} , whose elements f_{ij} represent the effect of variable i on performance trait j ; we note that these values are also referred to as the performance gradients for phenotypic traits (Arnold 1983). Each element of \mathbf{F} can be quantified, for example, as the

slope estimate from a multiple regression model that includes performance-determining traits as the independent variables and performance as the dependent variable (Ghalambor et al. 2003; Walker 2007). Performance trade-offs resulting from the functional architecture of the system can be captured by the off-diagonal elements of the product of the \mathbf{F} matrix and its transposed matrix ($\mathbf{F}^T\mathbf{F}$ matrix; Walker 2007). We explored the effects of adding performance-determining traits (rows) to the \mathbf{F} matrix, which we equate with increasing the level of complexity of the performance traits on the resulting trade-offs.

We extended the framework of Ghalambor et al. (2003) and Walker (2007) to incorporate the effects of covariance between performance-determining traits because covariance among these traits can also lead to trade-offs between performance variables even when they are not expected based on functional architecture (i.e., $\mathbf{F}^T\mathbf{F}$) alone (app. A; Rice 2004). Thus, we modeled performance trade-offs, described in the matrix \mathbf{P} , as

$$\mathbf{P} = \mathbf{F}^T\mathbf{C}\mathbf{F}, \quad (1)$$

where \mathbf{C} is the variance-covariance matrix for the morphological or functional traits and contains the variances for traits on the diagonal and covariances between them elsewhere (for derivation see app. A).

To investigate the general response of performance trade-offs to increasing complexity (fig. 2), we used numerical simulations. We started with a simple functional system composed of one morphological (or functional or physiological) trait (m_1) that affects two performance traits (P_1 and P_2) where a strong trade-off exists so that $f_{11} = -f_{12}$. We then increased functional complexity by sequentially adding traits (m_2 through m_{10}) to which we independently and randomly assigned effect sizes, f_{i1} and f_{i2} , by sampling from a continuous uniform distribution ($-1, 1$). Each additional trait can affect each performance P_1 and P_2 in the same direction (if the sign of f_{i1} is the same as that of f_{i2}), can result in a trade-off (if the sign of f_{i1} is different from that of f_{i2}), or can affect one performance trait only (if either f_{i1} or f_{i2} equals 0).

We repeated the numerical simulations 1,000 times for each level of complexity under two different treatments to the \mathbf{C} matrix. First, to examine the effects of increasing complexity when all performance-determining traits are equally variable and independent of one another, we fixed the \mathbf{C} matrix to be an identity matrix (1's in the diagonal and 0's elsewhere). Second, we simulated a correlation structure between the performance-determining traits to represent the case in which correlations between traits change when traits are added to the functional system. Under this scenario, we repopulated the entire \mathbf{C} matrix each time we increased complexity (i.e., added a trait). Details on how the \mathbf{C} matrix was constructed with realistic

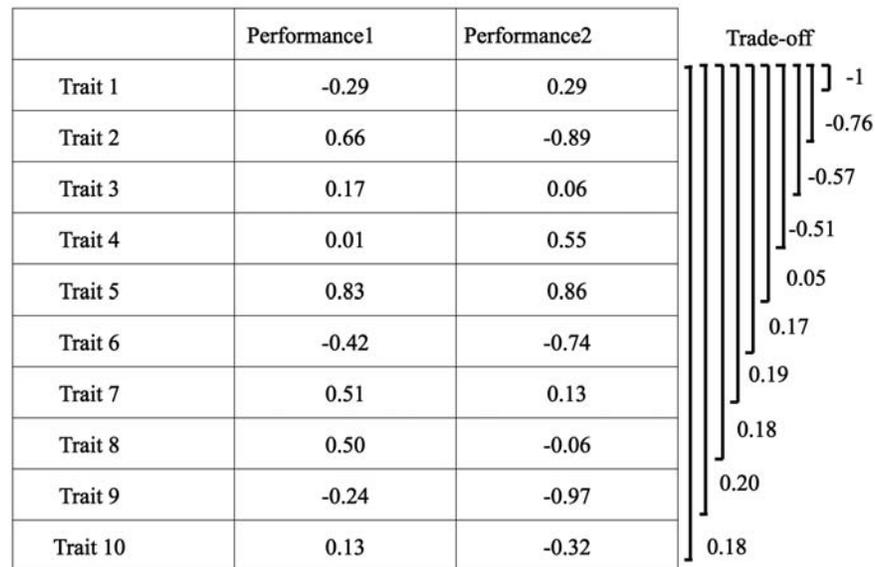


Figure 2: Effect of functional complexity on performance trade-offs illustrated using an F matrix with 10 performance-determining traits (*rows*) and two performance traits (*columns*). Each cell in the table represents the effect of each trait on each performance variable expressed as the partial regression coefficients from a multiple regression model. In this example, we simulated the F matrix by randomly drawing the trait effect for each cell from a continuous uniform distribution $(-1, 1)$. The performance trade-off is given for increasing levels of complexity (defined as the number of performance-determining traits in the F matrix). The trade-off for each level of complexity n was calculated from the F matrix with traits 1 through n . For example, the trade-off in a system with four traits (-0.51) was calculated by matrix multiplication of the 4×2 F matrix composed of rows 1–4 by the transposed matrix, F^T .

covariance structure between traits are in appendix A. Correlations calculated from the C matrixes ranged between -1.0 and 1.0 and had a mean absolute value of 0.4 .

Overview of Empirical Estimates for Suction Feeding Trade-Offs in Centrarchid Fishes

As an empirical test of the hypothesis that functional complexity mitigates performance trade-offs, we estimated trade-offs between suction feeding performance variables in centrarchid fishes and compared these values to those expected if performance were determined by a simpler feeding mechanism. For each of 15 species of centrarchid fishes, we quantified species values for functional variables, performance traits, and diet. We focused on three functional variables underlying feeding performance: flow speed, gape size, and mouth displacement speed. We then estimated species values for the force exerted on the prey and the spatial reach of the induced water flow. These variables describe mechanical performance, but we were also interested in obtaining more integrated measures of feeding ability. Therefore, we also evaluated feeding performance on attached and evasive prey as capture success rates inferred from a hydrodynamic model and as empirical data on the contribution of these prey types to species

diets. Given these data and a robust fossil-calibrated molecular phylogeny of the Centrarchidae (Near et al. 2005), we calculated phylogenetically independent contrasts for all variables to account for covariance that results from shared evolutionary history among species (Felsenstein 1985). We used independent contrasts for functional, performance, and diet variables to examine the following relationships: (1) the effects of mechanical performance traits (reach of suction flows and the force exerted on the prey) on dietary performance (strike success rates on attached and evasive prey), (2) the trade-off between the two mechanical performance traits (reach of suction flows and the force exerted on the prey), and (3) the trade-off between the two dietary performances (feeding on attached vs. evasive prey). We evaluated the above relationships based on both hydrodynamic model inferred success rates and diet data.

In addition to these empirical relationships, we also evaluated the strengths of the adaptive relationships (1) and trade-offs (2 and 3) for simpler feeding mechanisms (i.e., those in which only one or two functional components determine feeding performance), which were determined by manipulating the hydrodynamic model such that some functional variables did not contribute to the observed variation in performance. Comparisons between

the observed trade-offs and those estimated for the simpler feeding mechanisms served as tests for the hypothesized effect of functional complexity on performance trade-offs.

Estimating Species Values for Functional Variables

For individual fish from each of 15 centrarchid species, we used a combination of morphological measurements and kinematic analysis of feeding strikes to determine flow speed, gape size, and mouth displacement speed. We estimated peak flow speed for each individual based on a combination of morphological variables that is directly proportional to a fish's maximal capacity to generate suction pressure inside its buccal cavity (referred to as a suction index; Carroll et al. 2004; Holzman et al. 2008c). Our use of a suction index to predict peak flow speed is based on hydrodynamic considerations (the Bernoulli principle; Muller et al. 1982; Vogel 1994) and empirical data (Higham et al. 2006b; Holzman et al. 2008c), which indicate that suction pressure can be approximated as peak flow speed squared. Given a fish's capacity to generate flow speed, suction feeding performance is further determined by the extent of mouth opening (Wainwright et al. 2007) and mouth displacement speed (the sum of jaw protrusion and swimming speed; Holzman et al. 2008b). Therefore, we also measured the maximal extent of mouth opening and the speed at which the mouth moves toward the prey, from high-speed videos of feeding strikes filmed in lateral view. Appendix B in the online edition of the *American Naturalist* contains additional information regarding the estimation and analysis of suction index, flow speed, and feeding kinematics.

Hydrodynamic Model Estimates of Suction Performance

We used observed and estimated values for the three functional variables (flow speed, gape size, and mouth displacement speed) and kinematics from actual feeding strikes to parameterize a model of water flow in front of the mouth and around the prey (Holzman et al. 2007; Wainwright and Day 2007; Holzman and Wainwright 2009). The hydrodynamic model is an empirically and computationally validated set of physical equations (Holzman et al. 2007; Wainwright and Day 2007; Van Wassenbergh and Aerts 2009) that uses observed functional variables and kinematics to estimate properties of the flow for suction feeding strikes. We applied this model to estimate the mechanical performance measures (force and reach), to predict capture success on attached and evasive prey and to determine the performance gradients for flow speed, gape size, and mouth displacement speed.

The framework for estimating the suction-induced flow field from strike kinematics is detailed elsewhere (Holzman

et al. 2007, 2008b) and will be briefly presented here. The temporal variation of flow in front of the fish's mouth is known to have a stereotypical pattern that is strongly linked to the timing of buccal cavity expansion (Higham et al. 2006a; Holzman et al. 2008c). Because strong correlations exist in our data between the time to peak gape and other cranial events that are related to buccal expansion (the time of peak hyoid depression [$r = 0.87$] and head elevation [$r = 0.93$]), the timing of mouth opening served as a proxy for the timing of buccal expansion, and we matched the time of flow initiation and peak flow speed to the gape cycle. In addition, the spatial pattern of flow is a function of the extent of mouth opening, and flow speed exhibits a predictable pattern of decay with distance from the center of the mouth (Muller et al. 1982; Higham et al. 2006a; Holzman et al. 2008c; Van Wassenbergh and Aerts 2009). Therefore, we defined the spatial reach of the flow as the distance from the center of the mouth to the point where flow speed drops to 5% of its value at the mouth opening.

The hydrodynamic force exerted on prey results from the differential speeds and accelerations between the prey and the water around it, as well as from a differential flow field across the prey (e.g., stronger flows closer to the mouth will exert a force in that direction). The hydrodynamic model used observed kinematics for the change in gape size and the distance between the prey and predator to calculate the flow speeds and accelerations at the prey in intervals of 0.3 ms, which allowed us to estimate the forces exerted on the prey as a function of time. We controlled for variation in prey size and shape by modeling the same prey dimensions (a shrimplike prey, 24 mm in length, 3 mm in maximum diameter) for all strikes in all individuals.

We also applied the hydrodynamic model to estimate species values for capture success on attached and evasive prey. For each observed strike, we used the flow pattern inferred from the hydrodynamic model to determine whether the fish would successfully capture an attached or an evasive prey item. Capture success on an attached prey item occurred when the hydrodynamic force on the prey exceeded a specified attachment force of 1.1×10^{-2} N (Wainwright and Day 2007; Holzman et al. 2008b), chosen such that capture rates were ~50% across all trials for all fish. To model evasive prey, we specified an escape trajectory oriented directly away from the fish involving a force of 6×10^{-4} N. This escape path is consistent with optimality considerations (Weihs and Webb 1984) and empirical observations of escaping shrimp (Arnott et al. 1999), copepods (Titelman 2001), and minnows (Weihs and Webb 1984), and the specified force is within the observed range for small evasive prey (Lenz and Hartline 1999; Buskey et al. 2002). Evasive prey were considered

captured when the suction-induced flow drew the prey into the mouth before the mouth closed.

Between-strike variation in the relative timing of cranial events has a strong effect on the strike's outcome (Wainwright et al. 2001; Holzman et al. 2007). For each run of the hydrodynamic model, we used the combination of cranial events as recorded in the kinematics of the observed strikes. This variation introduced intraspecific and intraindividual variation in the strike's outcome, which we included in our analysis by taking the mean frequency of successful strikes across individuals weighted by the number of strikes sampled within that individual.

Estimating Adaptive Relationships and Trade-Offs for Simplified Feeding Mechanisms

We also applied the hydrodynamic model to determine performance for simpler feeding mechanisms. In this context, simpler means fewer functional variables contribute to variation in performance. We evaluated performance trade-offs for all possible simplified feeding mechanisms as a general test of the effects of complexity on suction feeding performance evolution. We modeled six simplified systems—three in which a single trait contributed to the variation in performance and three in which two traits contributed to the variation in performance. For the single-component systems, we used the observed variation in one performance-determining trait (e.g., gape size) as the only source of functional variation in the system. This was done by scaling the other two performance-determining traits (e.g., mouth displacement and flow speed) to the first (e.g., gape) according to their predicted values based on the empirically derived regression equation relating each trait pair for all Centrarchidae (based on phylogenetically independent contrasts; see below). For the two-component systems, we scaled only one performance-determining trait at a time, preserving the observed variation in two performance-determining traits.

Quantifying the Amount of Attached and Evasive Prey in Species Diets

We quantitatively described the diets of 22 centrarchid species based on a synthesis of published gut content analyses (for full species list, see table C1 in the online edition of the *American Naturalist*). We combined data from studies that reported the percent numerical contribution of taxonomic prey categories (hereafter referred to as “numerical contribution”), and for each species we averaged over variation in season, locality, and size classes above adult body size. For analyses involving both mechanical performance and diet variables, we retained the 14 species from this data set that overlapped with the data set for

strike kinematics and force estimates. The median number of individual stomachs sampled per species was 116 (table C1). We excluded taxonomic prey categories that contributed to less than 5% of the total number of prey items for a species. This method provided species' values for a suite of 19 taxonomic prey categories, which were then assigned to functional groups based on their predominant habitat and antipredator behavior. Categories were attached prey (Diptera, Hemiptera, Trichoptera, Ephemeroptera, Coleoptera, Odonata, Gastropoda, and Bivalvia) and evasive prey (fish, crayfish, decapod shrimp, and Mysidacea).

Statistical Analysis

We used standardized phylogenetically independent contrasts to account for covariance between species values that result from phylogenetic relatedness (Felsenstein 1985). We applied a species-level, time-calibrated multilocus molecular phylogeny for Centrarchidae (Near et al. 2005) as the basis for calculating independent contrasts for all variables in the “ape” module of the statistical software R (R Development Core Team 2009). Appropriate standardization of independent contrasts was verified by confirming a lack of correlation between the absolute value of contrasts and the square root of their branch lengths (Garland et al. 1992). We interpreted independent contrasts to reflect the amount of evolutionary change in variables estimated for each node of the centrarchid phylogeny and hereafter refer to the relationships between evolutionary changes in functional, performance, and diet variables.

Because there was error in both response and predictor variables, we analyzed relationships between independent contrasts using major axis regression (Garland et al. 1992) implemented in the “smatr” module in R (R Development Core Team 2009). All regressions were forced through the origin, as is required for regressions involving independent contrasts (Garland et al. 1992).

To estimate the relative contributions of gape size, flow speed, and mouth displacement speed to the evolution of the force exerted on the prey, we used multiple least squares linear regression. The response variable of the model was force exerted on prey, and the predictors were the three force-determining components. We tested for normality of residuals and linearity of the relationship between predictors and the response and found no evidence that these model assumptions had been violated.

To test the hypothesis that complexity mitigates performance trade-offs, we quantified trade-off intensity between the two mechanical performance traits (force and reach) and between the two dietary axes (attached and evasive prey) as the coefficient of correspondence, r , from major axis regressions, and compared estimates of r in the

observed complex system and the simulated simple systems. However, comparing the r values between the two types of systems may be a weak test because the ability to detect a significant difference between estimates of r depends not only on the difference between the estimates but also on their magnitudes (Cohen 1988). For example, if $r_1 = 0.5$ and $r_2 = 0.25$, the power to detect a difference is only about one-fourth of the power to detect a difference when $r_1 = 0.9$ and $r_2 = 0.65$, even though the absolute difference (0.25) is the same (Cohen 1988). Therefore, we quantified the power to detect a significant difference in r using Cohen's scaled effect size q , which is the difference between two scaled r estimates; that is, $q = z_1 - z_2$, where

$$z_i = 0.5 \times \log_e \frac{1 + r_i}{1 - r_i}. \quad (2)$$

An effect size of 0.1 was considered to be a “small” difference, 0.3 indicated “medium,” and 0.5 indicated a “large” difference (Cohen 1988). Power was calculated for a one-tailed distribution, following the a priori hypothesis that complexity would mitigate trade-offs and therefore that r would be higher for the simple system than for the observed complex system. In cases of unequal number of observations, sample size to calculate power (n') was determined as

$$n' = \frac{2(n_1 - 3)(n_2 - 3)}{n_1 + n_2 - 6} + 3. \quad (3)$$

Except for the manual calculation of Cohen's effect size q and the power to detect a difference in r , statistical analyses were performed in the software package R (R Development Core Team 2009).

Results

Performance Trade-Offs in Simulated Functional Systems

Our numerical simulations indicate that increasing the number of traits that contribute to two performance traits reduces the intensity of the trade-off between them (figs. 2, 3). This general result is robust to variation in the correlation structure between performance-determining traits. Allowing correlations between traits to change with each additional trait, the expectation for mean trade-off intensity was identical to the case where traits were free to evolve independently, but the variance around the mean was higher for each level of complexity (fig. 3). Given these simulated results, we tested whether increasing complexity can mitigate performance trade-offs in an empirical data set.

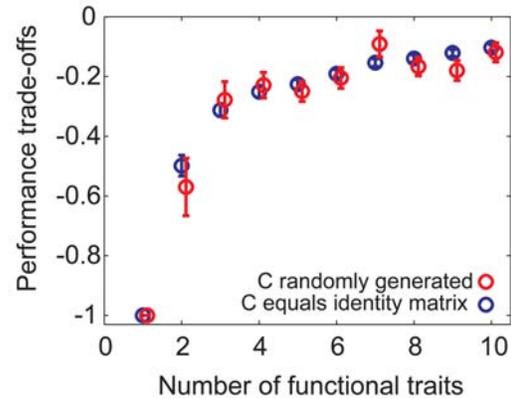


Figure 3: Effects of complexity (number of traits that determine performance; X-axis) on performance trade-offs (slope of the regression between two performance traits; Y-axis), for simulated functional systems contributing to two hypothetical performance variables. Point estimates for the performance trade-off at each level of complexity are means from 1,000 simulation replicates of the F matrix for the two treatments of the C matrix. Blue circles are for the case where traits evolve independently (*C equals identity matrix*). Red circles are for the case where the correlations between each pair of traits are restructured when new traits are added (*C randomly generated*). Error bars are standard errors. Red symbols are horizontally shifted for clarity of presentation.

Performance Gradients for Functional Variables Involved in Suction Feeding

We evaluated performance gradients for functional traits (flow speed, gape size, and mouth displacement speed) on performance variables (capture success rates on evasive and attached prey) based on the slope estimates from multiple regressions involving independent contrasts. For evasive prey, change in each functional trait had a similar effects on performance, but for attached prey, the main contributor was flow speed, followed by gape size and mouth displacement speed (table 1). The covariances between evolutionary changes in performance-determining traits (described in the C matrix) were low, indicating that changes in any one trait are not strongly linked with changes in other traits (table 1).

Effects of Complexity on the Evolution of Suction Performance

To investigate the effects of complexity on performance trade-offs, we simulated suction feeding performance for all three one-component systems and for the three possible combinations of two-component systems. We then contrasted the trade-off between the two mechanical performance traits (reach of suction flows and the force exerted

on the prey) and between the two dietary performances (feeding on attached vs. evasive prey) for the simple and the complex systems. We found a general trend of decreasing feeding performance trade-offs with increasing complexity (fig. 4). Both the mechanical performance trade-off and diet trade-off (inferred from the model) decreased with increasing complexity. Notably, the performance trade-offs for the observed, complex feeding mechanism were substantially weaker than those inferred for any of the simpler systems.

In addition to demonstrating the general effect of complexity on performance trade-offs, we examined in detail the contrast between the observed, complex system and a simple system in which only one performance-determining trait changes, in this case, gape size (figs. 5–7). In this simple system, the hydrodynamic model predicts that increases in force capacity enhance success of strikes on attached prey (major axis regression through origin, $r = 0.82$; $P = .0002$; fig. 5A), and increases in the spatial reach of flow speed increase success of strikes on evasive prey ($r = 0.54$; $P = .043$; fig. 5B). These results highlight the adaptive consequences of increased force and reach. However, the simple system exhibits a severe trade-off between the spatial reach of suction flows and the force exerted on prey ($r = -0.76$; $P < .0001$; fig. 6A). This mechanical trade-off results in a strong trade-off between strike success on attached and on escaping prey ($r = -0.76$; $P = .0012$; fig. 7A).

In contrast, our hydrodynamic model predicts that these trade-offs are substantially weaker in the observed system, in which gape, flow speed, and mouth displacement speed evolve to affect suction performance. We found equally strong positive correlations between force and strike success on attached prey ($r = 0.88$; $P < .0001$; fig. 5C) and between reach and strike success on evasive prey ($r = 0.8$; $P < .0003$; fig. 5D), while the trade-off between the spatial reach of suction flows and the force exerted on the prey was much weaker ($r = -0.54$; $P = .042$; fig. 6B).

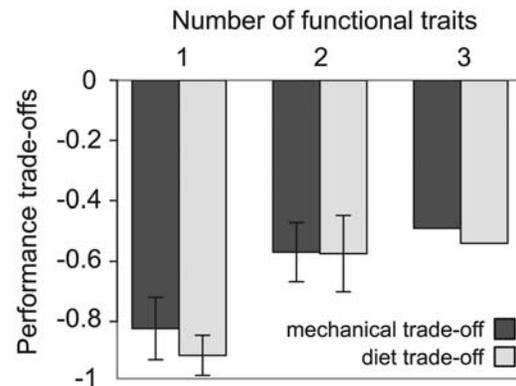


Figure 4: Effects of complexity on suction performance trade-offs, derived from hydrodynamic model inferred performance for systems with varying number of performance-determining traits. Data are mechanical (force vs. reach) and diet (success on attached vs. evasive prey) trade-offs derived from the hydrodynamic model. Trade-offs were quantified as the slope of the regression between force and reach (black bars) and strike success on attached and evasive prey (gray bars). Data for the one- and two-component systems are means (\pm SD) for the three possible combinations in each category. Trade-offs for the three-component system are the values estimated for the observed system (see figs. 6, 7).

Concomitantly, only nonsignificant correlations and lower-magnitude r estimates typified the relationship between strike success on attached and on evasive prey ($r = -0.49$; $P = 0.078$; fig. 6B).

We validated results from our hydrodynamic model's simulated strike success rates by demonstrating similar patterns based on the amounts of attached and evasive prey in centrarchid species' diets. As predicted, we found strong positive correlations between the evolution of force and changes in the proportion of attached prey in the diet ($r = 0.83$; $P = .0003$; fig. 5E) and between reach and the proportion of evasive prey in the diet ($r = 0.61$; $P = .003$; fig. 5F). However, we found weak nonsignificant cor-

Table 1: The F and C matrices for the three suction-determining traits and their effects on feeding performance on attached and evasive prey

	F		C		
	Escaping	Attached	Gape	Flow speed	JP
Gape	.224	-.027	1	-.083	.13
Flow speed	.124	.401	-.083	1	.26
Mouth displacement	.088	.0027	.13	.26	1

Note: Each cell in F represents the effect of each performance-determining trait (gape, flow speed, mouth displacement) on feeding performance on attached and evasive prey, expressed as the slope obtained from a multiple regression model involving independent contrasts. The C matrix describes the correlations between independent contrasts for each pair of traits. The performance trade-offs resulting from the system are plotted in figures 6 and 7. JP = jaw protrusion.

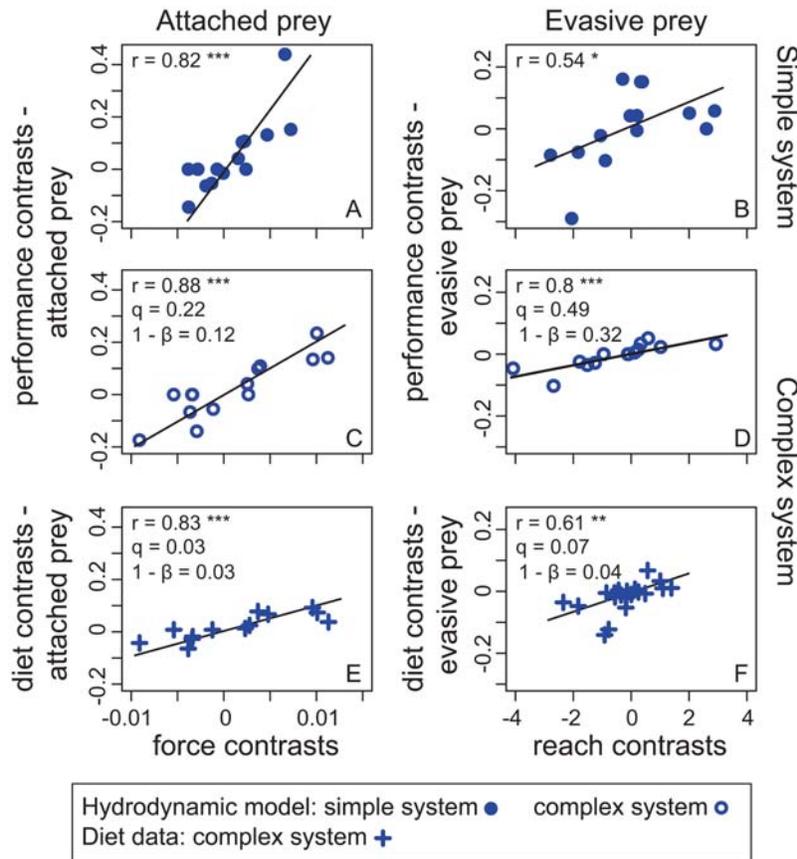


Figure 5: Complexity and adaptation for prey capture in centrarchid fishes. The ability to exert higher suction forces on prey increases the success rate of capturing attached prey based on hydrodynamic model inferred performance for simple (A) and complex (C) feeding systems and based on compilation of diet data (E). Similarly, increased spatial reach of suction flows increases the success rate in capturing evasive prey (B, D, F). In the simple system (A, B), only one functional component (gape) determines variation in performance, whereas in the observed complex system, performance is affected by three components (gape, flow speed, and mouth displacement speed). Correlations based on the hydrodynamic model (C, D) closely reflect those based on compilation of diet data (E, F). Points are phylogenetically independent contrasts derived from centrarchid species values and the Near et al. (2005) phylogeny for the Centrarchidae. Asterisks denote significance levels for the hypothesis that slope = 0: three, $P < .001$; two, $P < .01$; one, $P < .05$. Effect size q is the scaled difference between the r value of the simple system and each of the complex ones; q values of 0.1 indicate “small” difference, 0.3 indicate “medium,” and 0.5 indicate “large” differences (Cohen 1988); $1 - \beta$ is the power to detect an effect size q .

relations between changes in reach and the amount of attached prey ($r = -0.45$; $P = .11$) and between changes in the dietary contributions of attached and evasive prey ($r = -0.06$; $P = 0.79$; fig. 7C).

We calculated Cohen’s D and effect size q in order to estimate the power necessary to detect a significant reduction in r values (Cohen 1988) in complex compared to simple systems. For the adaptive relationships (fig. 5) effect sizes were mostly small ($q < 0.3$) with low power to detect a difference between simple and complex system (ranging between 0.03 and 0.32), indicating that the adaptive mechanisms that underlie feeding performance are similar for our complex and simple systems. However, on

the trade-off axes (figs. 6, 7) effect sizes were medium ($q > 0.3$) and large ($q > 0.5$) with much higher power (between 0.24 and 0.66) to detect a difference in trade-off intensity between simple and complex system, supporting our hypothesis that complexity in the functional basis of suction feeding mitigates trade-offs between performance axes.

Discussion

We found support for the hypothesis that in complex functional systems, performance costs that result from competing demands on one trait (i.e., trade-offs) can be mit-

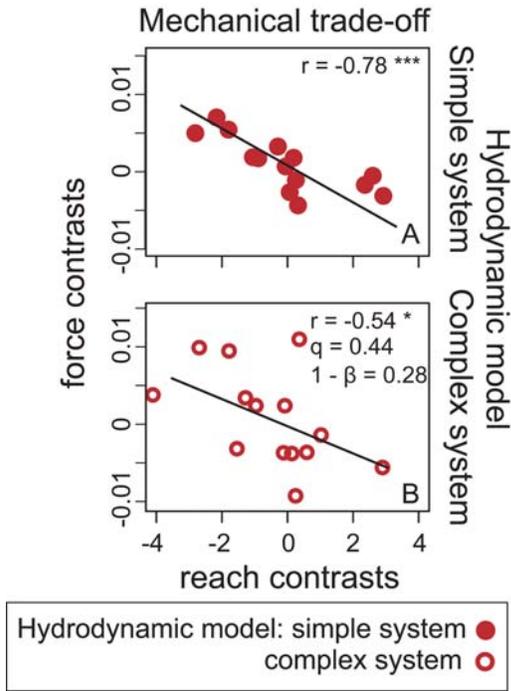


Figure 6: Contrast of the trade-off between force and reach in a simple system and the observed complex system. For a simple system (A) in which only gape determines the hydrodynamic force on the prey, a strong trade-off exists between force and the spatial reach of suction flow because increases in force necessarily involve reduction in gape and concomitant reduction in reach. This trade-off is greatly reduced in the observed complex system (B), in which three factors determine the force exerted on the prey and costs inflicted by increasing gape size can be mitigated by changes in other traits. Performance contrasts are phylogenetically independent contrasts derived from 15 centrarchid species values for force and reach inferred from the hydrodynamic model parameterized with observed strike kinematics for those species (A, B). Notations for significance levels, the power to detect effect size ($1 - \beta$), and effect size q are given in the legend for figure 5.

igated by compensatory changes in other traits. The suction feeding mechanism in centrarchid fishes illustrates how multiple traits underlying performance allow adaptive evolution to proceed without steep costs to other performance axes and thereby weaken the constraining effects of trade-offs (fig. 2). Across centrarchid fishes, evolutionary increases in gape size enhance the reach of suction-induced flows and result in increases in the amount of evasive prey in the diet, while the negative effect of increasing gape size on suction forces does not result in a decrement in the ability to feed on attached prey. This weakening of the impact of the feeding performance trade-off occurs because other functional traits (mouth displacement and flow speed) evolve independently of gape to increase force and enhance effectiveness of feeding on at-

tached prey. We suggest that, in general, trade-offs will be less prevalent and less constraining to the evolution of performance in complex systems.

Although evolutionary trends toward increasing complexity have been documented in multiple biological sys-

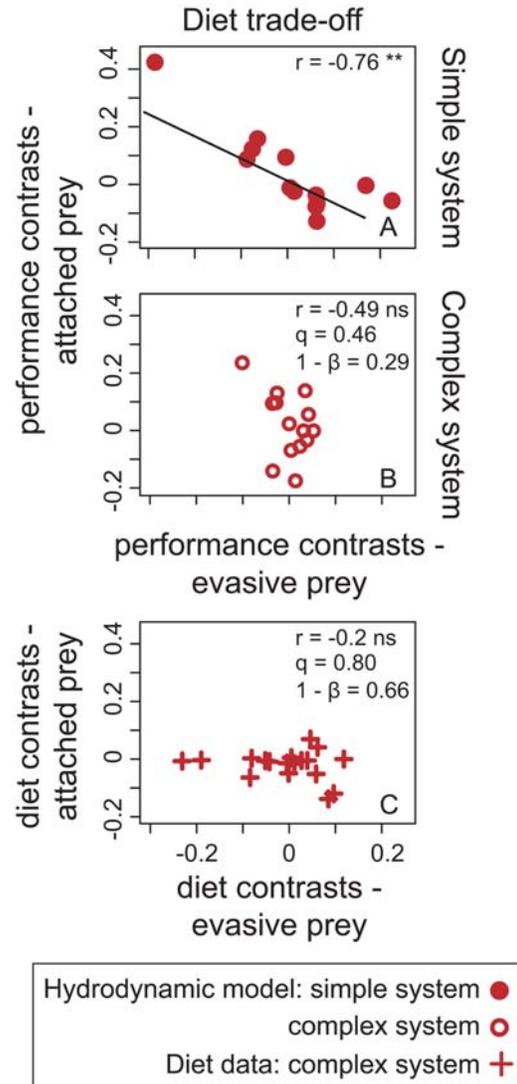


Figure 7: Dietary performance trade-offs in complex versus simple systems. For the simple system (A), a strong performance trade-off between the ability to feed on attached and evasive prey is observed due to the trade-off between reach and the ability to exert force on attached prey (fig. 4). This trade-off is greatly reduced in the observed complex system (B). The weak trade-off based on hydrodynamic model inferred performance (B) closely reflects the trade-off based on data for the contribution of these prey to species diets (C). Points are phylogenetically independent contrasts derived from centrarchid species values and the Near et al. (2005) phylogeny for the Centrarchidae. Notations for significance levels, the power to detect effect size ($1 - \beta$), and effect size q are given in the legend of figure 5.

tems, hypotheses concerning the role of complexity in driving macroevolutionary patterns of organismal diversification remain contentious (McShea 1996; Carroll 2001; Avise and Ayala 2007; Hazen et al. 2007; Adamowicz et al. 2008). Based on the results of this study, we suggest that for complex performance traits, trade-offs may not be a necessary consequence of multiple performance demands. For example, Bennett and Lenski (2007) found the surprising result that thermal adaptation in *E. coli* was not always associated with a fitness cost at low temperatures. Similarly, weak (though statistically significant) trade-offs were observed between stages of pregnancy and burst-swimming performance in guppies (Ghalambor et al. 2004). We speculate that complexity in the mechanisms underlying thermal tolerance (Bennett and Lenski 2007) and locomotory performance (Ghalambor et al. 2004) could explain such examples of weak or absent trade-offs when strong trade-offs are expected. Similar to the feeding system in centrarchids, the evolution of traits underlying adaptation to high temperatures may be accompanied by independent evolution of multiple traits that lessen costs to performance at low temperatures (Bennett and Lenski 2007).

The capacity for complexity to mitigate trade-offs may allow for simultaneous increases in multiple performance traits, even when those performance traits share morphological or functional components that affect them in opposite ways. Compared to the simpler systems, the observed feeding mechanism of centrarchids exhibits a disproportionate number of increases in feeding performance on both attached and evasive prey; independent contrasts for 7 (of 14) nodes infer increases in success on both evasive and attached prey (fig. C1 in the online edition of the *American Naturalist*). This pattern is mirrored in analyses involving diet contrasts (fig. C1). Similar phenomena have been observed in other functional systems and taxa. For example, in juvenile garter snakes, individuals that were able to achieve fast sprint speeds were also more likely to have better endurance (indicated by the positive association [$r > 0.35$] between the two traits; Jayne and Bennett 1990). In two subspecies of the Mediterranean lizards *Podarcis hispanica*, no trade-off between climbing and horizontal running was observed. On the contrary, *P. hispanica hispanica* individuals were better in sprinting, running, and climbing than the other subspecies, *P. hispanica atrata* (Van Damme et al. 1997). We hypothesize that complexity in the basis of sprinting, running, and climbing performance is likely a major factor permitting the evolution of combinations of high performance that appear to violate underlying trade-offs, producing phenotypes that excel in multiple tasks.

The evolutionary consequences of complexity that we describe here are similar to those of a well-studied phe-

nomenon known as functional redundancy, in which two or more traits that contributed to the same function in an ancestor have since diverged to specialize on different aspects of that function or to perform different functions altogether. This mechanism is well known in molecular evolution (where duplicate genes can rapidly diverge in their expression profiles; Chung et al. 2006), developmental biology (where gene duplication is thought to correlate with the duplication and increasing diversity of morphological features and body segments; Carroll 2001), and organismal functional design (where muscles are subdivided and modified to transmit force to different skeletal elements; Friel and Wainwright 1997). We suggest that functional redundancy is a special case of complexity that arises through duplication (Lauder 1990; Lynch and Conery 2003; Hughes and Friedman 2005) or evolution of novelties that take over an aspect of performance (Liem 1973; Gatesy and Middleton 1997). Redundancy increases the number of components that can evolve in combination to modify performance, thereby weakening trade-offs imposed by conflicting demands on those components. We argue that complexity is a more general concept than redundancy and duplication because the components underlying a complex performance trait may not have performed the same ancestral function. Nevertheless, because both complexity and redundancy weaken constraints imposed by trade-offs, the evolutionary consequences predicted for redundant functional systems may also apply to complex systems. Specifically, individual components of complex systems may evolve faster than components of simple systems.

Our results also suggest that complexity increases the potential for adaptive divergence in a clade because niche breadth may increase when trade-offs are weak. When increases in force are associated with limited cost to reach, species may increase the amount of attached prey in their diets without adversely affecting their ability to feed on escaping prey (fig. C1). Therefore, complex performance traits may allow niche expansion, whereas simple traits only permit niche shifts. For example, in Darwin's finches, a force-velocity trade-off drives divergence in beak size and bite force but also in beak closing velocity and vocal performance capacity (Herrel et al. 2009). In that case, the mechanical trade-off between force and speed provides a link between niche divergence and mating signal divergence, two features that have likely been important during the history of this radiation (Herrel et al. 2009). However, this force-velocity trade-off constrains morphological diversification in the sense that it allows performance to evolve only on the trade-off axis and limits changes in the orthogonal direction. In this way, complex performance traits may be characterized by flatter adaptive landscapes

than simple traits, which may make transitions between adaptive peaks more probable.

The capacity for complex traits to mitigate performance trade-offs also provides a functional explanation for “Liem’s paradox” (Liem 1984, 1990; Robinson and Wilson 1998), where extreme skull morphology is coupled with generalist feeding ecology. In Liem’s view, the weak relationship between morphological and ecological specialization was evidence that morphological diversity evolved for nonadaptive reasons, and he hypothesized that feeding versatility persists because it is adaptively neutral (Liem 1984, 1990). The apparent paradox was later resolved by other researchers who pointed out that phenotypic specializations are required only for specific prey types that may not be preferred when other intrinsically “non-demanding” prey are abundant (Robinson and Wilson 1998). The latter model predicts “the most extreme phenotypic specializations should occur in the absence of a trade-off between using preferred and non-preferred resources” (p. 223). Whereas this resolution to Liem’s paradox centers on the demands imposed by prey, we suggest that, in some cases, functional complexity may provide an alternative mechanism that weakens dietary trade-offs. By limiting the costs to other aspects of feeding performance, complexity may enable morphologically extreme species to effectively utilize a wide range of prey items.

In some cases, though, we expect correspondence between extreme morphology, performance, and ecological specialization. For example, a pipefish could not crush corals as effectively as a triggerfish even if it showed a similar level of skull complexity (most skeletal elements constituting the skull of both fishes are the same). Oppositely, a triggerfish cannot be as effective as a pipefish for feeding on planktonic copepods. This is because extreme performance capabilities may require specific combinations of structural and functional traits providing little flexibility for their modification for other functions (Alfaro et al. 2005). For example, the highest forces exerted on prey will be achieved by species that maximize suction pressure capacity, maximize mouth displacement speed, and minimize gape diameter. An increase in gape in such a force-modified species would necessarily incur a cost to force capacity because neither suction pressure nor displacement speed can be increased. Therefore, we also hypothesize that specialist species with extreme performance capabilities may suffer more severe trade-offs than generalist species with intermediate performance.

Complexity and the Evolution of Suction Feeding Performance

We found only a weak, nonsignificant trade-off between the ability to dislodge attached prey and the ability to

capture evasive ones, based on a model of water flow that we parameterized using observed feeding kinematics. This result is in agreement with the observed relationship between these prey types that was based on a compilation of centrarchid species diet data (fig. 7). Although the concordance between performance based on the hydrodynamic model simulations and empirical data for species diets provides evidence that the weak relationship between these dietary axes is a consequence of the functional architecture underlying suction feeding performance, an alternative explanation is that fish may use their jaws to bite the prey off the substrate. This behavior is particularly common when fish encounter large nonmotile food items that have to be scraped from the substrate, as observed in parrotfishes when feeding on the algal mats on corals, or when triggerfish use teeth to tear off parts of the prey (Wainwright and Bellwood 2002; Westneat et al. 2005). High-speed video of largemouth bass and bluegill feeding in the lab on attached prey (pieces of squid, shrimp, and fish eggs glued to a pressure transducer) indicate that these fish use suction to try to dislodge the prey (Holzman et al. 2007, 2008a). Similarly, Ferry-Graham et al. (2002) reported that ram and suction dominated feedings on attached prey in wrasses, which possess a more pronounced set of teeth than centrarchids. In addition, we have observed a range of species of pomacentrids (damselfishes) and serranids (sea basses and groupers) using mainly suction when feeding on prey held firmly in an attached clip (R. Holzman and P. C. Wainwright, unpublished data). We therefore favor the explanation that the trade-off between capturing attached and evasive prey is mitigated by complex basis of suction performance; however, our current data cannot rule out the additional influence of behaviors such as biting.

Because suction feeding performance is underlain by many interacting morphological and functional traits, we suggest that this complexity may alleviate feeding performance trade-offs that would otherwise constrain evolution in many groups of suction feeding vertebrates. However, our results do not imply a general absence of a trade-off between the ability to feed on evasive and attached prey. Indeed, data for turtles reveal a substantial trade-off between these performance and dietary axes (Herrel et al. 2002). Although this result is attributed to other traits (the ability to quickly retract the head into the shell) rather than the biomechanical basis of suction production, the difference in trade-off intensity between turtles and centrarchids may be due to differences in complexity of suction performance. Turtles lack many of the features that have a strong effect on the patterns of flow in front of the mouths of fishes (Lauder 1980, 1985; Holzman et al. 2008b); these include a circular mouth aperture, opercular slits, the ability to protrude their jaws, and overall cranial

kinesis. Therefore, feeding performance evolution in turtles may be driven by fewer underlying morphological and functional traits.

To parameterize our hydrodynamic model, we used morphological and kinematic proxies rather than direct measurements because the relevant empirical data (e.g., maximal flow speed, timing of peak flow speed, and cranial muscles' activation patterns) are available for only a handful of centrarchid species. The functional basis of feeding performance is likely more complex than modeled here. For example, evolutionary changes in muscles that expand the buccal cavity, particularly those that contribute to lateral expansion of the skull, may also vary in ways that mitigate suction performance trade-offs. Similarly, we used suction pressure as a proxy for flow speed under the assumption that the temporal pattern of peak flow speed is conserved across centrarchids, though the strength of the relationship may vary among species. We see these simplifications as conservative factors with respect to our hypothesis because they result in an underestimate of the complexity of feeding performance. Although we acknowledge that our assumptions have led us to ignore some functional variables that contribute to performance and thus make the feeding mechanism more complex than portrayed here, our simplified version is an apt demonstration that complex performance traits are less constrained by trade-offs.

Our study also found strong evidence for the adaptive consequences of two mechanical measures of suction feeding performance: suction-induced reach of the flow and force on the prey. The demonstrated adaptive relationship between reach and performance on evasive prey is concordant with previous hypotheses and observations. An association between large gape and feeding on evasive prey has been well documented in fishes (Werner 1977; Keast 1985; Wainwright and Richard 1995; Westneat 1995; Collar et al. 2009), but the effect of gape size on the spatial reach of the flow has only recently been documented (Day et al. 2005; Holzman et al. 2008c). Here, we show that greater reach is associated with enhanced success rates of capturing evasive prey based on hydrodynamic model-inferred performance and increased proportions of evasive prey in the diet (fig. 5). We note, however, that the reach of the flow is highly correlated with other mechanical measures of suction performance that are likely relevant to capturing evasive prey, particularly the volumetric rate of flow and ingested volume of water (Higham et al. 2006b). In contrast, the adaptive role of strong suction pressures and the resultant high flow speeds and accelerations (and ultimately large forces on the prey) have been less clear. One previous hypothesis suggested that large suction pressures enabled fish to draw prey into the mouth from farther away (Norton and Brainerd 1993), though later studies

showed that no association exists between suction pressure and strike distance (Wainwright et al. 2001; Svanback et al. 2002). Subsequent work has shown that the force exerted on the prey can be decomposed into contributions from suction pressure (the pressure gradient force), flow velocity (drag force), and flow acceleration (acceleration reaction force; Wainwright and Day 2007; Holzman et al. 2008a). Because the latter two components are relevant only when water is moving past the prey, increased capacity to produce high flow speeds and accelerations have been hypothesized to increase performance on prey that attempt to avoid capture by clinging to substrates (Wainwright and Day 2007; Holzman et al. 2008a). This hypothesis is clearly supported by our results based on both model-inferred performance on attached prey and data for the contribution of attached prey to centrarchid species diets.

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