
BEHAVIORAL CHARACTERS AND HISTORICAL PROPERTIES OF MOTOR PATTERNS

PETER C. WAINWRIGHT¹ AND JOHN P. FRIEL²

¹*Department of Evolution and Ecology, University of California, Davis, CA 95616*

²*Cornell University Museum of Vertebrates, Department of Ecology and Evolutionary Biology,
Ithaca, NY 14853*

INTRODUCTION

Organismal behavior has long been a controversial source of systematic characters (Brown, 1975; Masterton *et al.*, 1976; Brooks and McLennan, 1991; de Queiroz and Wimberger, 1993; Houch and Drickamer, 1996) that has never enjoyed the popularity of anatomy or DNA. This lack of popularity has both practical and philosophical causes. The chief practical obstacle is the difficulty in obtaining adequate observations on large numbers of taxa (Wenzel, 1992; Greene, 1994). Some authors have argued that behavioral characters are fundamentally poorly suited to use in systematics because they are plastic and often variable (Klopfer, 1969, 1975; Atz, 1970; Hailman, 1976; Aronson 1981), but in this chapter we take the point of view that neither attribute eliminates behavior as a source of useful characters (see also Lauder, 1986, 1994; Wenzel, 1992; de Queiroz and Wimberger, 1993; Greene, 1994). Although the effort involved in obtaining sufficient observations to assess behavioral characters in large numbers of species is likely to limit their widespread utility in systematics, we anticipate that studies of the evolution of focal behavioral traits will enjoy a dynamic future.

In this chapter we explore the properties of one type of behavioral data in some detail, motor patterns, when viewed in a phylogenetic context. In effect we ask if motor pattern characters distilled from behavioral observations can be shown empirically to contain phylogenetic information. We cover two major issues. First, we ask whether motor patterns (patterns of muscle activation that underlie movement) meet the criteria for potentially useful systematic characters. Second, two decades of comparative research on the evolution of the lower vertebrate skull and the behaviors associated with the skull permit a number of useful generalizations about the properties of these motor pattern variables and how to deal with them when searching for historical patterns. Our thesis is that behavioral variables are frequently phylogenetically informative but they require special attention to their description and variability. We illustrate the major conclusions that have come from research in this area with examples from our own research on behavioral evolution in tetraodontiform fishes.

The key property of a systematic character that establishes its utility in phylogenetic analysis is that similarity among taxa is due to homology. Thus a fundamental issue regarding the potential use of behavioral traits in systematics revolves around the problem of establishing homology of behaviors. This topic has been discussed recently by others (Lauder, 1986, 1994; Wenzel, 1992; Greene, 1994). Here we concur with Wenzel (1992) and take the view that "determining homology among behaviors is no different than determining homology among morphological structures". As with any character type, the utility of behavioral characters is best tested in the context of the total suite of characters that can be brought to bear on a phylogenetic problem (Patterson, 1982). Useful or informative characters will be those that tend to unite natural groups, and show relatively little convergence. Characters that tend to show unique states in each taxon of a clade, like any autapomorphy, will contribute little to resolving phylogenetic relationships.

The effort involved in obtaining thorough behavioral observations on large numbers of taxa will greatly limit the utility of behavior as a source of characters for use in systematic analyses. For this reason it is not our intention to argue for the extensive use of behavior in systematics, but instead we emphasize that phylogenies can be used to study the history of those behavioral traits that have the properties of good systematic characters. It is in the use of the phylogenetic perspective to study the evolution of animal behavior and its component elements that we expect to see the greatest returns from viewing behavioral traits as systematic characters (Greene and Burghardt, 1978; Paul, 1981a, 1981b, 1991; Lauder, 1986, 1983; McLennan *et al.*, 1988; Gittleman, 1989; Schreck and Throckmorton, 1989; Losos, 1990; McLennan, 1991; Brooks and McLennan, 1991; Schultz, 1992; Alves-Gomez and Hopkins, 1997; Wainwright and Turingan, 1997).

There are many ways that behaviors can be measured in such a fashion that the resulting metrics can be treated as characters with discrete states (Wenzel, 1992; Greene, 1994). As behaviors are particularly complex with several

underlying components, one approach is to consider the various levels of activity that create animal movement (Paul, 1991; Stridter and Northcutt, 1991). Reilly and Lauder (1992) drew a useful distinction between kinematic patterns (physical movement), motor patterns (activity of muscles that cause movement), and morphology as three levels of animal behavior. Although theoretical considerations permit predictions about how modifications of morphology in specific systems are likely to affect kinematic patterns given a constant motor pattern (Barel, 1983; Westneat, 1990; Richard and Wainwright, 1995), it remains a relatively unstudied question the extent to which these components of behavior are independent (Reilly and Lauder, 1992; Smith, 1994). In this chapter we focus our examples and comments on muscle activity patterns because a substantial body of literature exists that examines historical changes in muscle activity patterns, but we expect our comments to apply more broadly to the evolution of kinematics and other components of behavior.

We use the term "motor pattern" to refer to patterns of muscle contraction that drive the behavior under study. Muscular contraction can be documented by several methods, ranging from direct measurements of muscle shortening to extracellular electrical recordings of muscle cell depolarizations, or electromyography. Electromyograms (Fig. 1) include information about the time course of nervous stimulation of muscles and the intensity of the stimulation (Loeb and Gans, 1986). By simultaneously determining the activity of several muscles, the relative activity period for each muscle can be determined. Often it is this sequence of muscle contraction that is of primary interest in studies of motor pattern. The data that we discuss here will all be of this latter type.

Triggerfish Feeding on Fiddler Crab

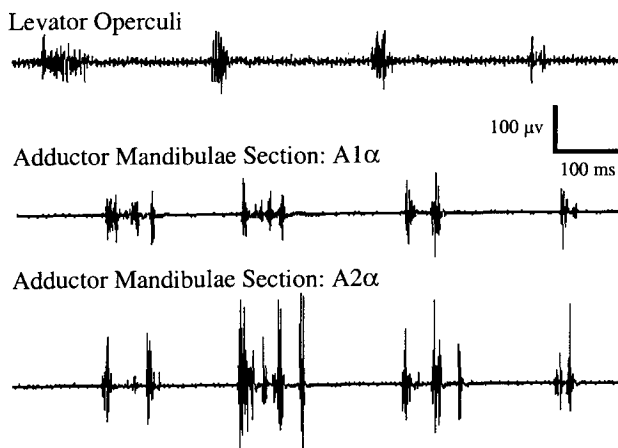


Figure 1 Sample electromyogram of three muscles from a gray triggerfish, *Balistes capriscus*, feeding on a fiddler crab (*Uca* sp.). Each channel shows a record of voltage against time from a different muscle during several cycles of buccal manipulation behavior.

We distinguish motor patterns from "kinematic patterns," or the movements associated with animal behavior. Motor patterns represent the nervous stimulation of muscles that create kinematics. Note that some authors have used the term "motor pattern" to refer to what we define as kinematic pattern (Marler and Hamilton, 1966; Kardong, 1997), but our intention is to distinguish between these two elements of animal behavior. Candidate kinematic parameters that may evolve and be valuable characters include any aspect of motion that can be defined in context and measured. Thus, phylogenetically meaningful patterns could potentially be found in a variety of traits such as the angular excursion of a limb element during running, the extent of opening of the mouth during prey capture in a fish, or the time course and sequence of events in a complex movement such as tentacle projection by cephalopod molluscs during prey capture. Kinematic data can be collected by recording film or video sequences of animals executing behaviors. Image-by-image analysis of motion can then be conducted on the recordings to produce data on the extent, direction, and time course of motion. Typical kinematic variables distilled from recordings of prey capture in lower vertebrates might be the angular rotation of the jaws, the extent of mouth opening, the angle of dorsal rotation of the head, and the extent of forward body movement during the prey capture sequence. As noted earlier, motor patterns interact with the mechanical properties of the stiff elements of anatomy (e.g., bones or muscular hydrostats) to produce kinematic patterns.

Regardless of what type of behavioral trait is being studied there are a number of advantages to quantifying the qualities of interest and subjecting them to analyses that capitalize on the wealth of tools embodied within parametric statistics (Zar, 1984; Sokal and Rohlf, 1985). Traits that are measured are more easily defined, and as behaviors are frequently influenced by numerous external stimuli it is crucial to be able to partition sources of variance when comparing behaviors across taxa.

EVOLUTION OF MOTOR PATTERNS IN THE SKULL OF TETRAODONTIFORM FISHES

We present two examples from our studies of behavioral evolution to illustrate the methods for analyzing motor patterns that have been developed in the past two decades and to illustrate some general results that have emerged concerning the evolution of muscle activation patterns. The first example involves a comparison of the activity pattern of a jaw adductor muscle in four species of tetraodontiform fishes. This case study focuses on the activity pattern of a single muscle and is used to illustrate steps in evaluating motor pattern evolution: methods of quantifying the activation pattern of the muscle, methods for comparing trait values across species, and the biological insights gained from such a comparison.

In the second example we review a study of the evolution of inflation behavior in pufferfishes and the role of motor pattern changes in the acquisition of this extraordinary behavior. This case study places motor pattern evolution into the broader context of behavioral evolution and illustrates several general results that have emerged from studies of motor pattern evolution: motor patterns are conservative during evolution and yet distinct modifications can be identified that had a key role in the origin of this novel behavior.

Activity Patterns of the Adductor Mandibulae Muscle in Tetraodontiform Fishes

The teleost order Tetraodontiformes is a cosmopolitan group of marine fishes made up of nine families, including such recognizable and divergent groups as the triggerfishes, (Balistidae), filefishes, (Monacanthidae), boxfishes, (Ostraciidae), pufferfishes, (Tetraodontidae and Diodontidae), and ocean sunfishes (Molidae). Tetraodontiform feeding is characterized by the use of a small mouth equipped with stout teeth and jaws that are controlled by well-developed musculature to grasp and reduce prey. In using direct oral jaw biting extensively during feeding these fishes differ from generalized teleosts which typically rely heavily on suction feeding for prey capture (Turingan and Wainwright, 1993).

Figure 1 shows a typical electromyographic recordings of the adductor mandibulae section 2 α (hereafter A2 α) and two other jaw muscles during four cycles of manipulation of a crab prey by a gray triggerfish, *Balistes capriscus*. Feeding triggerfish, like other tetraodontiforms, repeatedly bite their prey as they attempt to remove small pieces and generally reduce the prey to segments that can easily be swallowed. This behavior, termed buccal manipulation, involves repeated cycles of activity in the jaw adductor muscles. Each cycle of biting is associated with a discrete burst of activity in the adductor muscle. The activity pattern of the adductor mandibulae muscle and its antagonists drive this behavior and interact with the skeletal system to produce the biting movements.

We focus here on activity of section A2 α during buccal manipulation. We quantified each burst of A2 α activity by measuring the duration of the burst, the average amplitude of the electrical spikes (intensity), and the timing of the burst relative to a reference muscle, the levator operculi, which is active during jaw opening.

For this analysis we recorded and analyzed electromyograms during feeding by individuals of four tetraodontiform species: the planehead filefish (*Monacanthus hispidus*), the gray triggerfish (*Balistes capriscus*), the Southern puffer (*Sphoeroides nephalus*), and the striped burrfish (*Chilomycterus schoepfi*) (see also Friel and Wainwright, 1998). Recordings were made from four individuals per species (for burrfish N = 3) feeding on three prey types. The prey, live panaeid shrimp, live fiddler crabs, and pieces of squid mantle, were chosen to present different escape abilities and toughness during biting. An

average of 80 cycles of buccal manipulation behavior were recorded from each individual fish feeding on each prey type for a total of 6,837 cycles of activity analyzed in the entire data set. We compared the motor pattern variables across four species using an experimental design that partitioned variance from several sources: variation among species, among individuals, among prey type, and the interactions between the main effects. The overall experimental design was a two-way ANOVA (Species crossed with Prey Type) with Individuals nested within Species. This design also includes two interaction terms, Species X Prey Type and Individuals X Prey Type.

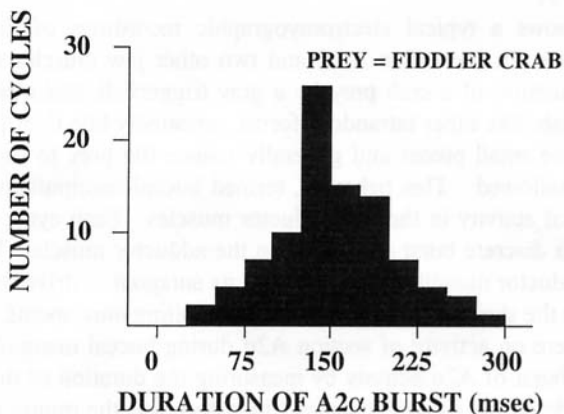


Figure 2 Frequency histogram of the burst duration of the A2 α muscle. Data represent 93 cycles of muscle activity from four individual gray triggerfishes, *Balistes caprisicus*, feeding on fiddler crabs (*Uca* sp.). Note that the value of this motor pattern trait is highly variable, as is typical of EMG variables taken from fish feeding behaviors. The variable has a mean of 152 milliseconds and a standard deviation of 52, for a coefficient of variation of 0.34.

The frequency distribution of a typical variable (e.g., burst duration) from this analysis is shown in Fig. 2. Note the broad range of values and high variance found for the burst duration of the A2 α muscle. Table I reports the ANOVA results for the Species and Prey Type main effects run on the three variables that describe the activity pattern of the A2 α muscle. There are significant species effects on the onset time and duration of the burst of activity, but not on the intensity of the burst. Post-hoc pairwise comparisons revealed that for both onset time and burst duration the burrfish differs from each of the other three species, but these other three species do not differ from each other.

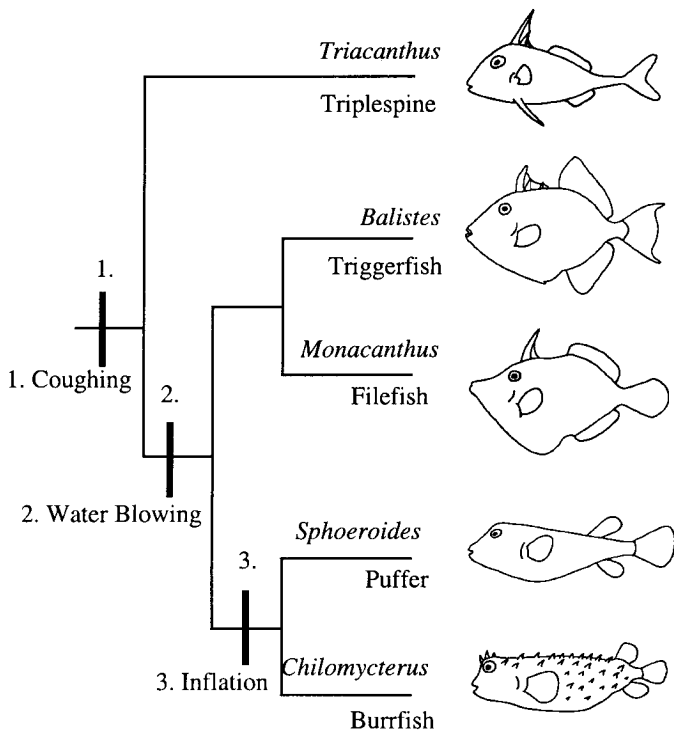


FIGURE 3 Phylogenetic relationships of the five tetraodontiform species studied by Wainwright and Turingan (1997). The distribution of the three oral compression behaviors is indicated by the numbered bars. 1. Coughing behavior is found in all tetraodontiform species as well as other teleost fishes. 2. Water blowing behavior is found in triggerfishes, filefishes, cowfishes (not shown), and members of the puffer lineage. 3. Inflation behavior is exhibited by all members of the two pufferfish families, the Tetraodontidae and the Diodontidae. As tetraodontiforms appear to retain a more plesiomorphic ability to cough, there are no anatomical specializations for this behavior in the order. There are also no anatomical novelties associated with water blowing behavior in the group above *Triacanthus*. In sharp contrast, inflation behavior is associated with a suite of major morphological modifications, including hypertrophied muscles and bones, and kinetic pectoral girdle and a novel mechanism for depression of the floor of the mouth.

If we consider A2 α onset time and burst duration to be two characters, each can be resolved into two character states from this analysis. On average, burrfish exhibit a significantly longer burst of activity in the A2 α that has a later onset than seen in the other three species. If we "map" these two characters on a phylogeny of the four species (see Fig. 3 for a phylogeny of these taxa) it becomes apparent that activity of the A2 α muscle is conserved through most of the tetraodontiform clade, while both traits show state changes and are autapomorphic for burrfish. At present neither character would contribute to resolving questions about relationships between these four taxa because both show a single state change that is unique to the burrfish. In other words, these characters do not suggest natural groupings within the four taxa. However, the characters do suggest the hypothesis that burrfishes and other diodontids exhibit a derived pattern of activity in the A2 α muscle. This hypothesis could be explored in additional species within the burrfish clade.

These data illustrate three general features of motor patterns of the lower vertebrate skull. (1) Motor patterns are highly variable, (2) individual fish exhibit considerable control over them, and yet despite these two points (3) motor patterns show a strong tendency for conservation across species.

Figure 2 is a histogram of 93 cycles of buccal manipulation activity from four gray triggerfish feeding on fiddler crabs. Burst duration of the A2 α muscle ranged from 54 to 298 milliseconds, with a mean of 154 ms and a standard deviation of 52. The coefficient of variation of this variable is 0.34. Despite this variability the triggerfish mean of 154 ms was found to be significantly different from the burrfish mean of 218 ms, though not different from the filefish or pufferfish means (119 and 132 ms, respectively).

The significant effects of prey type on burst onset and burst duration illustrate a result that is typical to studies of the effects of prey on motor patterns. Virtually every teleost fish species that has been studied quantitatively has shown the ability to modify muscle activation patterns in response to prey type (Liem, 1979; Sibbing, 1982; Lauder, 1983; Sibbing *et al.*, 1986; Wainwright and Lauder, 1986; Sanderson, 1988; Wainwright and Turingan, 1993; Ralston and Wainwright, 1997; Wainwright, 1989; Friel and Wainwright, 1998). As indicated earlier, an important implication of this result is that interspecific comparisons of muscle activity must either account for prey type effects or hold this variable constant. In some cases species also differ in how they respond to prey type (Friel and Wainwright, 1998), a more subtle way that motor patterns may differ between taxa.

The result that activity of the A2 α muscle is unchanged in three of the taxa also highlights a general finding. Previous interspecific studies of muscle activity patterns in feeding lower vertebrates have shown that, within fairly closely related groups (e.g., confamilial species), feeding motor patterns tend to be strongly conserved in that tests of the species effect with ANOVAs typically find

significance in fewer than 15% of EMG variables (see also Wainwright, 1989; Lauder and Shaffer, 1993; Smith, 1994).

Evolution of inflation behavior in pufferfishes

Our second case study concerns the motor basis of pufferfish inflation behavior and its evolutionary origins (Wainwright and Turingan, 1997). All species in the two tetraodontiform families Tetraodontidae (smooth-skinned puffers) and Diodontidae (spiny puffers) have the remarkable ability to inflate their body with water, a behavior these slow swimming fish use to deter predators. Inflation is accomplished by the fish pumping several mouthfuls of water into its stomach. The stomach of puffers and the ventral skin of the body are modified to permit the tremendous volume change and expansion that occur as the animal inflates itself (Brainerd, 1994; Wainwright *et al.*, 1995). However, here we focus on the mechanism of the oral pump that is used by puffers to repeatedly draw water into the mouth and pump it through the esophagus and into the stomach.

The sequence of events that occurs in a single pumping cycle begins with expansion of the oral cavity and opening the mouth to permit water to flow in. The mechanism of oral expansion is a novelty of pufferfishes and involves a suite of substantial anatomical modifications that permit the pectoral girdle to swing posteriorly, simultaneously with depression of the ventral region of the mouth by flexion of the hyoid apparatus. Once the oral cavity is full of water these actions are reversed: the mouth is closed and the ventral mouth region and pectoral girdle are elevated and protracted respectively. A stout oral valve is located just behind the jaws and helps to prevent water from escaping back out the mouth during oral compression. Instead the esophagus is relaxed and water is pumped through it into the stomach. This is followed immediately by another cycle of the same actions.

Among tetraodontiform fishes there are at least two additional behaviors that have similarities to the inflation pump and are phylogenetically more broadly distributed. All tetraodontiform fishes, indeed virtually all fishes, possess the ability to "cough." This is a behavior in which fishes expel unwanted material from the mouth by rapidly compressing the oral cavity and using the water flow to carry the debris away. Many tetraodontiform fishes also actively "blow" water jets out of their mouth and use the pulses of water to manipulate the environment. Perhaps the most spectacular use of water blowing is seen in many triggerfishes who will use water jets to expose prey that are buried in sand, and to manipulate large prey such as sea urchins that must be rolled over to expose the more vulnerable oral surface before the fish can successfully attack and consume them (Fricke, 1971, 1975; Frazer, 1991). Like inflation behavior, coughing and water blowing involve a cyclical pattern of oral expansion, when water is drawn

into the mouth, and oral compression, when water is forced out of the mouth. The key difference is that during coughing and water blowing the mouth is held open during the compression phase, to permit water to rapidly exit the mouth, while the mouth is closed during the compressive phase of inflation to prevent water loss out the mouth.

The distribution of these three behaviors on a simplified phylogeny of tetraodontiform fishes (Fig. 3) suggests that the three behaviors may represent a transformation series. Coughing is seen in all tetraodontiform taxa, and more broadly in other teleosts as well. Water blowing is not known to occur in the Triacanthoidea, the sister group to all other tetraodontiforms. However, it does occur in all other tetraodontiform families. Finally, inflation has the most restricted distribution, being found only in puffers. A hypothesis that follows from the phylogenetic distribution of these behaviors is that water blowing and inflation behavior are increasingly specialized behaviors that evolved from coughing. This hypothesis has been explored by mapping the anatomical and motor pattern traits associated with these behaviors onto an independently derived cladogram of tetraodontiform fishes (Wainwright and Turingan, 1997).

There are five major results from the quantitative comparisons of muscle activity patterns and anatomical specializations associated with these three behaviors in the five tetraodontiform taxa shown in Fig 3. (1) The motor patterns of the three behaviors were similar, with only minor differences distinguishing them. (2) The motor pattern for coughing did not differ among the five tetraodontiform taxa. (3) The motor pattern for water blowing did not differ between the two species studied (gray triggerfish and southern puffer) but differed from the coughing motor pattern by a change in a single motor pattern character, the burst duration of one of the muscles that compresses to mouth cavity (the AP; Fig. 4). (4) The motor pattern for inflation differed from the water blowing pattern in showing a briefer burst of activity in the mouth opening muscle (the LOP; Fig. 4). (5) There appear to be no anatomical specializations associated with coughing or water blowing but there are numerous major anatomical modifications associated with inflation behavior.

In this case the motor pattern characters clearly support the nested phylogeny of this group of five taxa (Fig. 3), although we note that variation within each component clade (the different families) has not been explored. The broad similarity in motor pattern across the three behaviors supports the hypothesis that the three behaviors share a common functional basis with slight modifications to create water blowing and inflation from the primitive and ubiquitous coughing pattern. However, the three behaviors can be distinguished from each other by a single modification in each case (Fig. 4).

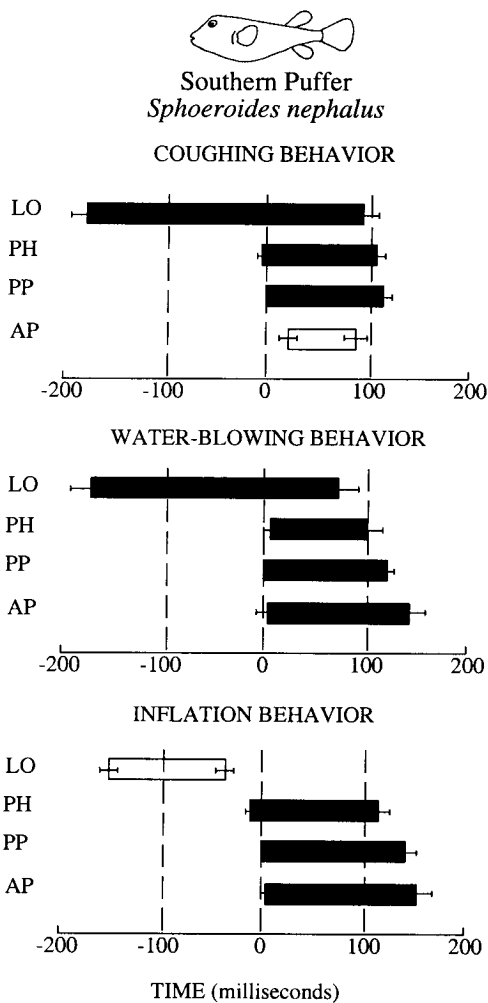


FIGURE 4 Patterns of activity for four cranial muscles during coughing ($N = 17$), water blowing ($N = 19$), and inflation behavior ($N = 48$) in four southern puffers, *Sphoeroides nephalus*. The length of bars indicates the mean burst duration of the muscle. Standard errors of burst duration are indicated to the right, while standard errors of relative onset time (onset times measured relative to the PP) are indicated to the left. Analyses of variance revealed that the motor pattern for these three behaviors is quite similar, but a single variable distinguishes coughing from the other two behaviors (AP burst duration) and a second variable distinguishes inflation from coughing and water blowing (LO burst duration). The LO muscle is the primary mouth opening muscle in these fishes and the reduced activity of it during inflation is associated with a major kinematic difference between the behaviors: during coughing and water blowing the LO muscle continues to contract into the compressive phase (indicated by activity of the PH, PP, and AP muscles), holding the mouth open so that water can be forced anteriorly. During inflation the mouth is closed during the compressive phase to prevent water from escaping out the mouth. This is indicated by the cessation of LO activity prior to the compressive phase.

HISTORICAL PROPERTIES OF MOTOR PATTERNS

We have illustrated with examples from our tetraodontiform research the observation that motor pattern parameters of the skull in aquatic lower vertebrates are highly variable within individuals and species. Further, this variability is under considerable control by the individual fish. Fish demonstrate an ability to respond to a wide range of environmental factors by modifying the motor patterns used during feeding behaviors. External factors such as prey type, prey position, and satiation level have all been shown to have significant effects on muscle activity patterns. Thus, the motor patterns involved in feeding are highly plastic and under considerable sensory control by the individual.

In the face of this tendency for high variability in motor patterns, quantitative analyses of feeding and related behaviors have, paradoxically, repeatedly found a strong tendency for patterns of muscle contraction to be conservative within fairly closely related groups of species, such as within families (Shaffer and Lauder, 1985; Wainwright and Lauder, 1986; Sanderson, 1988; Wainwright, 1989; Turingan and Wainwright, 1993; Friel and Wainwright, 1998). Although motor pattern characters are quite variable within individuals and within species, mean values tend to be similar across species. For example, our analysis of the activity of the A2 α muscle in four species of tetraodontiform fishes revealed that burst duration and burst onset time were significantly greater in the burrfish than in the other three species, but that there was no significant difference among the other three species in any of the three variables (Table I). The simplest interpretation of these results given the phylogenetic relationships among these taxa is that the average activity pattern of the A2 α muscle has been conserved across much of the tetraodontiform radiation.

Burst duration of the A2 α had means of 154, 119, and 132 ms, respectively, in the three species but variance was high in each species with coefficients of variation around 0.3 for every variable. Thus, high variance makes it difficult to distinguish the mean trait values in these three species. In fact, with sufficiently high sample sizes it may be possible to demonstrate that the mean burst durations differ. Calculations of power in these ANOVAs suggest that samples of over 30 individuals per species would be needed to distinguish these means, given the observed variability of the motor pattern. Nevertheless, reasonable sample sizes rarely show more than 10–15% of EMG variables differing significantly among closely related species while broader phylogenetic comparisons inevitably show a greater number of differences in motor pattern (e.g., Sanderson, 1988; Wainwright *et al.*, 1989; Wainwright and Turingan, 1997). Those differences in motor pattern that do occur, as in our analysis of muscle activity in oral compression behaviors by tetraodontiform fishes, are usually consistent with independent phylogenetic hypotheses. Empirically then, motor pattern traits associated with the skull tend to be conserved, though changes that are observed

frequently support independently derived phylogenies. No cases have yet to be reported of the convergent evolution of a distinct, derived motor pattern.

Table I Summary of Prey Type and Species effects on EMG variables of the A2a section of the adductor mandibulae muscle in triggerfishes (*Balistes*), filefishes (*Monacanthus*), pufferfishes (*Sphoeroides*), and burrfishes (*Chilomycterus*). Effects are based on univariate ANOVAs of EMG data recorded during prey processing of live fiddler crabs, pieces of squid tentacle, and live shrimps. Onsets for muscles are relative to the activity of the levator operculi. See also Friel and Wainwright, 1998.

EMG Variable	Prey Effect			Species Effect		
	<i>F</i> ratio	<i>df</i>	<i>P</i>	<i>F</i> ratio	<i>df</i>	<i>P</i>
Relative Onset	7.39	2,20	<0.01	4.24	3,10	0.04*
Duration	5.02	2,20	0.02*	7.96	3,10	<0.01
Relative Intensity	0.95	2,20	0.40	2.91	3,10	0.09

* = significant effects at α 0.05 level

Can a behavioral trait that is highly plastic be meaningfully argued to be evolutionarily conserved? We suggest that as long as (1) the conditions under which the trait is measured are controlled and defined and (2) the conclusion of conservation is based on a quantitative analysis that accounts for the measurable sources of variation, then findings of no significant interspecific difference are accurately interpreted as a conserved character (see also Wenzel, 1992; Greene, 1994; Lauder, 1994). The high intraspecific variance of motor pattern variables does suggest that increased sampling of individuals within species is likely to enhance the ability to discriminate species means that differ by up to 50%. This variability suggests that relative conservativeness or historical lability of behavioral traits should be based on observations from comparable numbers of individuals per species. However, the key point is that, even if intraspecific variation is high, adequate experimental design can result in a robust test of the hypothesis that the motor pattern trait is the same across the study taxa.

Why are average motor pattern trait values relatively conservative across species, given their high variability and the control that animals have over them? Particularly when the anatomy of the feeding mechanism is as different among species as in the case of the tetraodontiforms reported here (Fig. 3) one might expect to see modifications of the motor pattern that suit species-specific anatomy. Nevertheless, there are numerous striking examples of conserved motor patterns in clades of fishes that have undergone extensive anatomical evolution of the feeding apparatus and patterns of prey use (Sanderson, 1988;

Westneat and Wainwright, 1989; Wainwright and Lauder, 1992). Only in a few cases have workers been able to attribute a historical origin of a novel feeding ability or significant shift in feeding performance to changes in motor pattern (Liem, 1980; Lauder, 1983).

The best documented example of changes in motor pattern playing a central role in the origin of a novel feeding behavior concerns the origin of molluscivory in the freshwater sunfishes, Family Centrarchidae (Lauder, 1983). Two species of sunfish consume mostly molluscs in the wild, redear and pumpkinseed sunfish. These species are believed to be sister taxa (Mabee, 1993). In addition to possessing hypertrophied muscles and jaws used in mollusc crushing these species also exhibit a modified motor pattern that is used during the cracking of mollusc shells (Lauder, 1983).

Other work with centrarchids has found that the motor pattern used in prey capture has undergone only minor modification across a sample of four species that encompass the phylogenetic, morphological, and ecological range within the family (Wainwright and Lauder, 1986). For example, the motor pattern used during the capture of fish prey does not differ between the largemouth bass and bluegill sunfish, despite the fact that the morphology, feeding abilities, and patterns of prey use are different in these two species. Adult largemouth bass are specialized piscivores and bluegill are generalized invertebrate predators. Numerous phenotypic differences between the species have been identified that underlie the differences in feeding ability (summarized in Wainwright and Lauder, 1992). The body form and swimming abilities differ and the jaws of the largemouth bass are approximately 50% larger than the bluegill, have a different shape, and the mechanical properties of the lever system in the mandible differ between the two species (Wainwright and Richard, 1995). However, the two species use the same pattern of muscle activity when feeding on the same prey, despite a well-documented ability to modulate the motor pattern. This suggests the possibility that, across the rather broad range of anatomical designs of the feeding apparatus in sunfishes, the most effective motor pattern for prey capture is the same. Similarly, although the planehead filefish, gray triggerfish, and Southern puffer differ considerably in feeding morphology, they utilize the same activity pattern of the A2 α muscle.

Analyses of motor patterns often find differences among individuals within species to be a major source of variation, as in the studies reported here. However, it should be pointed out that to our knowledge there has never been an empirical attempt to measure the heritability of a motor pattern or kinematic trait. This would be a worthy research direction as a key assumption concerning characters that are used in systematics is that the variation one documents among taxa is heritable. It would also be valuable to know the extent to which motor pattern and kinematic traits are heritable as this will determine their potential for responding to natural selection.

We have presented one approach to quantifying and comparing behavior. An important goal of future research will be to compare the properties of motor

patterns to other types of behavioral traits, such as kinematic variables. Existing studies of feeding behaviors in aquatic feeding lower vertebrates suggest that kinematics show levels of variation comparable to, or slightly less than those seen in motor pattern traits (Shaffer and Lauder, 1985; Richard and Wainwright, 1995). For example, the time taken to completely open and close the jaws during prey capture in a representative 78-mm spotted sunfish, *Lepomis punctatus* (N = 108 feeding sequences), varied from 18 to 72 ms with a mean of 46 ms and a coefficient of variation of 0.24 (Wainwright, unpublished observations). Reilly and Lauder (1992) found comparable levels of variation in kinematic and motor pattern variables in several families of salamanders. It is tempting to believe that the profile of a single feeding sequence captures the key elements of the behavior, but the studies cited here of motor patterns and kinematics show the importance of adequately assessing variance in behavioral variables.

LITERATURE CITED

- Alves-Gomes, J., and Hopkins, C. D. (1997). Molecular insights into the phylogeny of mormyrid fishes and the evolution of their electric organs. *Brain Behav. Evol.* **49**:324-351.
- Aronson, L. R. (1981). Evolution of Telencephalic function in lower vertebrates. In "Brain Mechanisms of Behavior in Lower Vertebrates" (P.R. Laming, ed.), pp. 33-58. Cambridge University Press, Cambridge.
- Atz, J. W. (1970). The application of the idea of homology to animal behavior. In "Development and Evolution of Behavior: Essays in Honor of T. C. Schneirla" (L. R. Aronson, E. Tobach, D. S. Lehrman, and J. S. Rosenblatt eds.), pp. 53-74. W. H. Freeman, San Francisco.
- Barel, C. D. N. (1983). Towards a constructional morphology of the cichlid fishes (Teleostei, Perciformes). *Neth. J. Zool.* **33**:357-424.
- Brainerd, E. L. (1994). Pufferfish inflation: functional morphology of postcranial structures in *Diodon holocanthus* (Tetraodontiformes). *J. Morphol.* **220**:243-262.
- Brooks D. R., and McLennan, D. A. (1991). "Phylogeny, Ecology and Behavior." University of Chicago Press, Chicago.
- Brown, J. (1975). "The Evolution of Behavior." W. W. Norton, New York.
- de Queiroz, A., and Wimberger, P. H. (1993). The usefulness of behavior for phylogeny estimation: levels of homoplasy in behavioral and morphological characters. *Evolution* **47**:46-60.
- Frazier, T. K., Lindberg, W. J., and Stanton, G. R. (1991). Predation on sand dollars by gray triggerfish, *Balistes capriscus*, in the northeastern Gulf of Mexico. *Bull. Mar. Sci.* **48**:159-164.
- Fricke, H. W. (1971). Fische als feinde tropischer seeigel. *Mar. Biol.* **9**:328-338.
- Fricke, H. W. (1975). Losen einfacher probleme bei einem fisch (freiswasser an *Balistes fuscus*). *Zool. Tierpsychol.* **38**:18-33.
- Friel, J. P., and Wainwright, P. C. (1998). Evolution of motor pattern in Tetraodontiform fishes: does muscle duplication lead to functional diversification? *Brain Behav. Evol.* **53**:159-170.
- Gittleman, J. L. (1989). The comparative approach in ethology: aims and limitations. In "Perspectives in Ethology" (P. P. G. Bateson, and P. H. Klopfer, eds.), pp. 55-83. Plenum Press, New York.
- Greene, H. W. (1994). Homology and behavioral repertoires. In "Homology: The Hierarchical Basis of Biology" (B.K. Hall, ed.), pp. 369-381. Academic Press, San Diego.
- Greene, H. W., and Burghardt, G. M. (1978). Behavior and phylogeny: constriction in ancient and modern snakes. *Science* **200**:74-77.

- Hailman, J. P. (1976). Homology: logic, information and efficiency. In "Evolution, Brain and Behavior: Persistent Problems" (R.B. Masterton, W. Hodoss, and H. Jerison, eds.), pp. 181-198. Lawrence Erlbaum, Hillsdale, New Jersey.
- Houck, L. D., and Drickamer L. C. (1996). "Foundations of Animal Behavior: Classic Papers with Commentaries." University of Chicago Press, Chicago
- Kardong, K. V. (1997). Evolution of a motor pattern within squamates: the tell tale tongue. *Am. Zool.* **37**(5):81A.
- Klopfer, P. (1969). Review of R. F. Ewer, *Ethology of Mammals*. *Science* **165**:887.
- Klopfer, P. (1975). Review of J. Alcock, *Animal Behavior: An Evolutionary approach*. *Am. Sci.* **63**:578-579.
- Lauder, G. V. (1983). Functional and morphological bases of trophic specialization in sunfishes (Teleostei: Centrarchidae). *J. Morphol.* **178**:1-21.
- Lauder, G. V. (1986). Homology, analogy and the evolution of behavior. In "Evolution and Animal Behavior: Paleontological and Field Approaches" (M. H. Nitecki and J. A. Kitchell, eds.), pp. 9-40. Oxford University Press, Oxford.
- Lauder, G. V. (1994). Homology, form and function. In "Homologies: The Hierarchical Basis of Comparative Biology" (B. K. Hall, ed.), pp. 151-196. Academic Press, San Diego.
- Lauder, G.V., and Shaffer, H.B. (1993). Design of feeding systems in aquatic vertebrates: major patterns and their evolutionary interpretations. In "The Skull" (J. Hanken and B. K. Hall, eds.), Vol. 3. Univ. of Chicago Press, Chicago, IL.
- Liem, K. F. (1979). Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. *J. Zool. Lond.* **189**:93-125.
- Loeb, G.E., and Gans, C. (1986). "Electromyography for Experimentalists." University of Chicago Press.
- Losos, J. B. (1990). Concordant evolution of locomotor behavior, display rate and morphology in *Anolis* lizards. *Anim. Behav.* **39**:879-890.
- Mabee, P. M. (1993). Phylogenetic interpretation of ontogenetic change: sorting out the actual and artefactual in an empirical case study of centrarchid fishes. *Zool. J. Linn. Soc.* **107**:175-291.
- Marler, P., and Hamilton, W. J. (1966). "Mechanisms of Animal Behavior." John Wiley, New York.
- Masterton, R. B., Hodoss W., and Jerison, J. (1976). "Evolution, Brain, and Behavior: Persistent Problems." Lawrence Erlbaum Associates, Hillsdale, N.J.
- McLennan, D. A. (1991). Integrating phylogeny and experimental ethology: from pattern to process. *Evolution* **45**:1173-1789.
- McLennan, D. A., Brooks, D. R., and McPhail, J. D. (1988). The benefits of communication between comparative ethology and phylogenetic systematics: a case study using gasterosteid fishes. *Can. J. Zool.* **66**:2177-2190.
- Patterson, C. (1982). Morphological characters and homology. In "Problems of Phylogenetic Reconstruction" (K. A. Joysey and A. E. Friday, eds.), pp. 21-74. Academic Press, New York.
- Paul, D. H. (1981). Homologies between body movements and muscular contractions in the locomotion of two decapods of different families. *J. Exper. Biol.* **94**:159-168.
- Paul, D. H. (1981). Homologies between neuromuscular systems serving different functions in two decapod of different families. *J. Exper. Biol.* **94**:169-197.
- Paul, D. H. (1991). Pedigrees of neurobehavioral circuits: tracing the evolution of novel behaviors by comparing motor patterns, muscles and neurons in members of related taxa. *Brain Behav. Evol.* **38**:226-239.
- Ralston, K. R., and Wainwright, P. C. (1997). Functional consequences of trophic specialization in pufferfishes. *Funct. Ecol.* **11**:43-52.
- Reilly, S. M., and Lauder, G. V. (1992). Morphology, behavior, and evolution: comparative kinematics of aquatic feeding in salamanders. *Brain Behav. Evol.* **40**:182-196.
- Richard, B. A., and Wainwright, P. C. (1995). Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): kinematics of prey capture. *J. Exp. Biol.* **198**:419-433.

- Sanderson, S. L. (1988). Variation in neuromuscular activity during prey capture by trophic specialists and generalists (Pisces: Labridae). *Brain Behav. Evol.* **32**:257-268.
- Schultz, J. W. (1992). Muscle firing patterns in two arachnids using different methods of propulsive leg extension. *J. Exper. Biol.* **162**:313-329.
- Schwenk, K., and Throckmorton, G. S. (1989). Functional and evolutionary morphology of lingual feeding in squamate reptiles: phylogenetics and kinematics. *J. Zool. London* **219**:153-175.
- Shaffer, H. B., and Lauder, G. V. (1985). Aquatic prey capture in ambystomatid salamanders: patterns of variation in muscle activity. *J. Morphol.* **183**:273-284.
- Sibbing, F. A. (1982). Pharyngeal mastication and food transport in the carp (*Cyprinus carpio*): a cineradiographic and electromyographic study. *J. Morphol.* **172**:223-258.
- Sibbing, F. A., Osse, J. W. M., and Terlow, A. (1986). Food handling in the carp (*Cyprinus carpio*): its movement patterns, mechanisms and limitations. *J. Zool. Lond.* **210**:161-203.
- Smith, K. K. (1994). Are neuromuscular systems conserved in evolution? *Brain Behav. Evol.* **43**: 293-305.
- Sokal, R. R., and Rohlf, F. J. (1985). "Biometry." Freeman and Co., New York.
- Striedter, G. F., and Northcutt, R. G. (1991). Biological hierarchies and the concept of homology. *Brain Behav. Evol.* **38**:177-189.
- Turingan, R. G., and Wainwright, P. C. (1993). Morphological and functional bases of durophagy in the queen triggerfish, *Balistes vetula* (Pisces, Tetraodontiformes). *J. Morphol.* **215**:101-118.
- Wainwright, P. C. (1989). Prey processing in haemulid fishes: patterns of variation in pharyngeal jaw muscle activity. *J. Exp. Biol.* **141**:359-376.
- Wainwright, P. C., and Lauder, G. V. (1986). Feeding biology of sunfishes: patterns of variation in the feeding mechanism. *Zool. J. Linn. Soc.* **88**:217-228.
- Wainwright, P. C., Sanford, C. J., Reilly, S. M., and Lauder, G. V. (1989). Evolution of motor patterns: aquatic feeding in salamanders and ray-finned fishes. *Brain Behav. Evol.* **34**:329-341.
- Wainwright, P. C., and Turingan, R. G. (1993). Coupled versus uncoupled functional systems: motor plasticity in the queen triggerfish *Balistes vetula*. *J. Exp. Biol.* **180**:209-227.
- Wainwright, P. C., and Turingan, R. G. (1997). Evolution of pufferfish inflation behavior. *Evolution* **51**:506-518.
- Wainwright, P. C., Turingan, R. G., and Brainerd, E. L. (1995). Functional morphology of pufferfish inflation: mechanism of the buccal pump. *Copeia* **1995**:614-625.
- Wenzel, J. W. (1992). Behavioral homology and phylogeny. *Annu. Rev. Ecol. Syst.* **23**:361-381.
- Westneat, M. W. (1990). Feeding mechanics of teleost fishes (Labridae: Perciformes): a test of four-bar linkage models. *J. Morphol.* **205**:269-295.
- Zar, J. H. (1984). "Biostatistical Analysis." Prentice-Hall, Englewood Cliffs.