

Many-to-One Mapping of Form to Function: A General Principle in Organismal Design?¹

PETER C. WAINWRIGHT,² MICHAEL E. ALFARO,³ DANIEL I. BOLNICK,⁴ AND C. DARRIN HULSEY⁵

Section of Evolution and Ecology, University of California, Davis, California 95616

SYNOPSIS. We introduce the concept of many-to-one mapping of form to function and suggest that this emergent property of complex systems promotes the evolution of physiological diversity. Our work has focused on a 4-bar linkage found in labrid fish jaws that transmits muscular force and motion from the lower jaw to skeletal elements in the upper jaws. Many different 4-bar shapes produce the same amount of output rotation in the upper jaw per degree of lower jaw rotation, a mechanical property termed Maxillary KT. We illustrate three consequences of many-to-one mapping of 4-bar shape to Maxillary KT. First, many-to-one mapping can partially decouple morphological and mechanical diversity within clades. We found with simulations of 4-bars evolving on phylogenies of 500 taxa that morphological and mechanical diversity were only loosely correlated ($R^2 = 0.25$). Second, redundant mapping permits the simultaneous optimization of more than one mechanical property of the 4-bar. Labrid fishes have capitalized on this flexibility, as illustrated by several species that have Maxillary KT = 0.8 but have different values of a second property, Nasal KT. Finally, many-to-one mapping may increase the influence of historical factors in determining the evolution of morphology. Using a genetic model of 4-bar evolution we exerted convergent selection on three different starting 4-bar shapes and found that mechanical convergence only created morphological convergence in simulations where the starting forms were similar. Many-to-one mapping is widespread in physiological systems and operates at levels ranging from the redundant mapping of genotypes to phenotypes, up to the morphological basis of whole-organism performance. This phenomenon may be involved in the uneven distribution of functional diversity seen among animal lineages.

INTRODUCTION

There is a growing need to know why there is so much natural diversity in complex functional systems and why diversity is unevenly distributed among lineages of organisms. Progress in understanding diversity has come from several fronts. Comparative physiology has been central to this enterprise by characterizing the variety of forms in terms of their function, and often identifying the major axes of functional diversity (Bartholomew, 1981; Block *et al.*, 1993; Hochachka and Lutz, 2001; Huey and Bennett, 1987; Norberg, 2002; Streebman *et al.*, 2003). To understand why some groups have generated more physiological diversity than others, it has proven useful to consider the role of both environmental factors, such as the opportunities provided by the invasion of previously uninhabited landscapes (Baldwin and Sanderson, 1998; Farrell, 1998), as well as intrinsic properties of the organism itself (Lauder, 1981; Wake, 1982). Elements of the design of physiological systems may influence diversification, and thus, researchers have sought basic rules linking these two parameters (Lauder, 1990). An example of such a repeating theme is the key innovation—the idea that a functional innovation can have

a profound impact on the subsequent pattern of diversification within the clade that bears the novelty. Examples include the evolutionary success of beetle lineages that became phytophagous (Farrell, 1998), and the origin of flight in birds (Middleton and Gatesy, 2000; Ostrom, 1979). In spite of the appeal and potential importance of identifying general principles of organismal design, such as the key innovation, relatively few such concepts have been identified.

In this paper we identify a common property of physiological systems, many-to-one mapping of form to function, and we discuss its potential influence on the distribution of physiological diversity. We illustrate many-to-one mapping with examples from our recent work on the relationship between skeletal morphology and mechanical properties in the jaws of labrid fishes. While the specific examples we develop are drawn from our work with jaw mechanics in a single major group of fishes, we anticipate that the principles we describe will apply broadly to complex functional systems of interest in physiology, biomechanics and functional morphology, and at many different levels of analysis.

THE ORAL JAW 4-BAR LINKAGE OF LABRID FISHES

Fish skulls are highly kinetic, complex networks of contractile muscles that actuate motion of stiff skeletal elements through a variety of joints. While some parts of the moving skull can be modeled as operating like simple levers, several examples of 4-bar linkages have been proposed to operate, including a hyoid linkage (Anker, 1974; deVisser and Barel, 1996), an opercular linkage (Anker, 1974), and a linkage in the oral jaws (Westneat, 1990). Acting as complex levers, 4-bar linkages transmit muscular force and motion through

¹ From the Symposium *Integrative Biology: A Symposium Honoring George A. Bartholomew* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 5–9 January 2004, at New Orleans, Louisiana.

² E-mail: pcwainwright@ucdavis.edu

³ Present address: School of Biological Sciences, Washington State University, Pullman, Washington 99164.

⁴ Present address: Department of Integrative Biology, University of Texas, Austin, Texas 78712.

⁵ Present address: Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996.

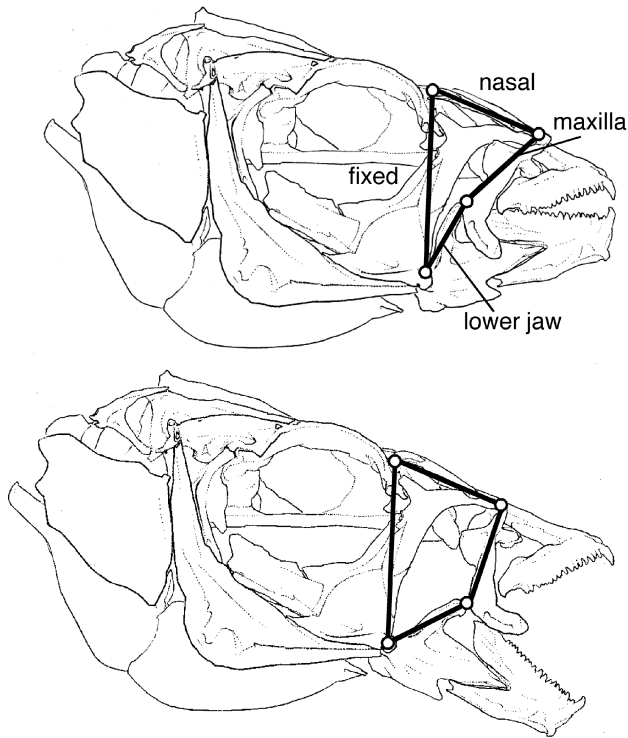


FIG. 1. Diagram of the oral jaws 4-bar linkage of labrid fishes using the example of *Oxycheilinus digrammus*. The system involves four skeletal elements (fixed link, nasal link, maxilla link and lower jaw link) connected together in a loop by joints that permit motion only in the plane of the page. As the lower jaw is rotated during opening, this motion is transmitted through the linkage to the maxilla, which pushes the upper jaw anteriorly. One way of describing the mechanical property of the linkage is the Maxillary KT, or the number of degrees of rotation in the maxilla per degree of input rotation of the lower jaw.

a series of four skeletal links that are connected together in a loop (Fig. 1). In the case of the oral jaws 4-bar linkage, the force and motion of muscles acting to rotate the mandible are transmitted to other parts of the linkage, such as the nasal bone and the maxillary bone. Because motion of the 4-bar is complex there are many different ways to characterize its mechanical properties. Previous work with this linkage in labrid fishes has focused on the effect of lower jaw rotation on movement of the maxilla, because the maxilla is intimately involved in controlling protrusion of the premaxilla (Westneat, 1995). Thus, one way to characterize the mechanical property of this linkage is with the Maxillary Kinematic Transmission Coefficient (Maxillary KT), which we define as the number of output degrees of rotation of the maxilla, relative to the position of the fixed link, for a given amount of input rotation in the lower jaw. Maxillary KT is therefore analogous to the inverse of mechanical advantage, the more familiar quantity that is typically used to describe the mechanical property of a lever system. Although Maxillary KT is but one property of the complex feeding apparatus, researchers have found that its value is significantly correlated with patterns of prey

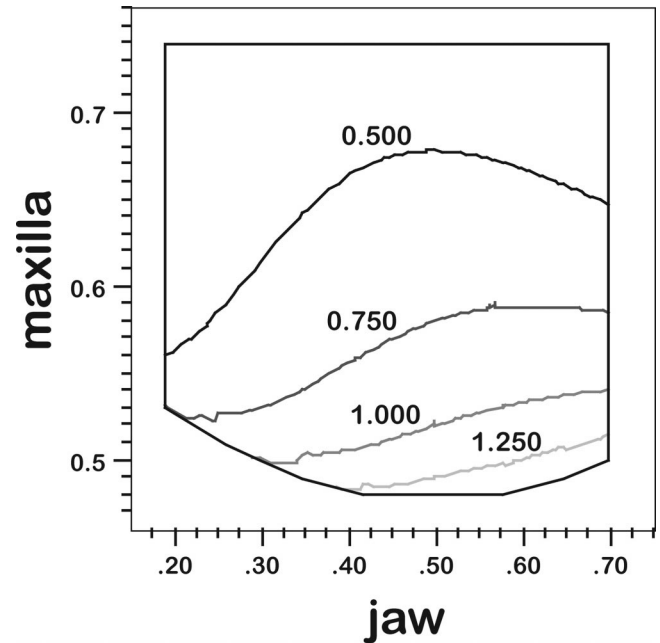


FIG. 2. Two dimensional slice through the 4-bar linkage morphospace with isoclines of constant Maxillary KT shown. Many different 4-bar shapes have each value of Maxillary KT. See also Hulsey and Wainwright (2002).

use in labrid fishes (Westneat, 1995; Wainwright *et al.*, 2004). Species with high Maxillary KT tend to feed on open-water zooplankton or elusive fishes and shrimps where they appear to capitalize on high motion transfer in the 4-bar. Labrids with low Maxillary KT that transmits more input force through the system typically feed on sessile benthic prey that may be captured by direct biting.

Maxillary KT is a function of the shape of the 4-bar, or the relative lengths of the four skeletal components. As with a simple lever system, the size of the system does not affect its mechanical property, only its shape does. The morphospace of all 4-bar linkage conformations can be visualized in three dimensions by expressing the length of each of the moving links as a fraction of the length of the fixed link (Hulsey and Wainwright, 2002). Figure 2 shows the part of this morphospace where the three moving links are all equal to or shorter than the fixed link. If the Maxillary KT is calculated for every 4-bar shape in this morphospace an important pattern emerges: there are many 4-bar shapes for every value of Maxillary KT (Hulsey and Wainwright, 2002). That is, there is a many-to-one mapping of morphology onto the mechanics of this system (Fig. 2). This many-to-one property of the 4-bar linkage is due to its relative morphological complexity. A simple lever system, once size is accounted for, has but a single pair of in-lever and out-lever lengths for each value of its KT. In the following sections, we explore important consequences of this many-to-one mapping on the evolutionary dynamics of the 4-bar system.

DYNAMICS OF 4-BAR LINKAGE EVOLUTION

Many-to-one mapping and the relationship between morphological and mechanical diversity

The redundant mapping of 4-bar shape onto Maxillary KT raises the possibility of a weak relationship between morphological diversity and diversity of Maxillary KT within groups of fishes. A common assumption in many ecomorphological analyses is that morphological diversity is a reasonable proxy for functional diversity. Many-to-one mapping suggests that considerable caution should be used when inferring this relationship.

We explored the dynamics of the relationship between morphological and mechanical diversity in the 4-bar linkage by simulating evolution of the four bars of the linkage on 1,000 randomly generated phylogenies of 500 tip taxa (Alfaro *et al.*, 2004). On each tree we simulated the evolution of the lengths of the four links of the 4-bar using a Brownian motion model of trait evolution. The four links were allowed to evolve separately, with checks at each change that the resulting conformation was a functional 4-bar. We started the simulation with an ancestral 4-bar drawn from a frequency histogram of the oral jaw 4-bars of 105 species of labrid fishes (Wainwright *et al.*, 2004). At the conclusion of each simulation we calculated the Maxillary KT for the 4-bar linkages of each of the 500 tip species. To measure morphological and mechanical diversity we calculated the variance in each trait among the 500 tip taxa (Foote and Gould, 1992). Morphological diversity was taken as the sum of the variance in the lengths of the four links of the 4-bar. Mechanical diversity was taken as the variance in the Maxillary KT of the 500 species in the tree. This exercise was repeated for each of the 1,000 phylogenies, with each tree generating a single value of morphological variance and a single value of mechanical variance (Fig. 3). Overall, morphological and mechanical variance was weakly, but significantly, correlated (R -square = 0.25).

A similar result was obtained when we calculated morphological and Maxillary KT diversity within nine presumed monophyletic groups of labrid fishes. In this case, there was no significant relationship between these variables. Some clades had high mechanical diversity and low morphological diversity, while other clades had high morphological diversity and low mechanical diversity (Hulsey and Wainwright, 2002; Alfaro *et al.*, 2004). The implication of these results is sobering for ecomorphological analyses that measure morphological diversity and interpret it as being representative of functional diversity. If many-to-one mapping is a common theme, it provides one reason why it is critical to measure directly the functional properties of interest when trying to assess functional diversity.

Many-to-one mapping permits optimization of multiple mechanical properties

Like many other parts of organisms, the oral jaws 4-bar linkage of labrid fishes contributes to other func-

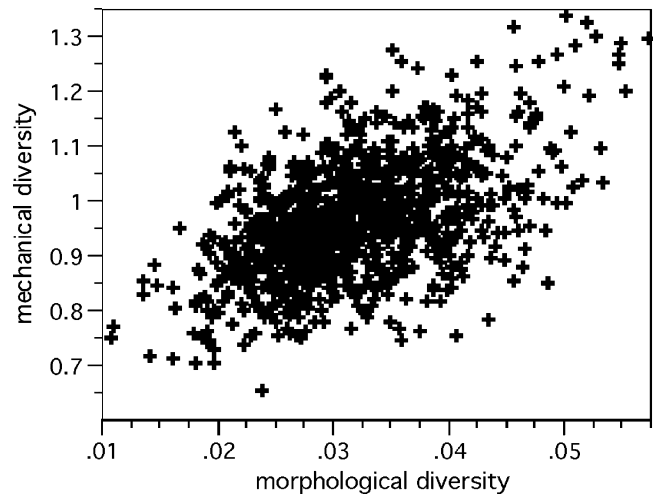


FIG. 3. Result from 1,000 simulations of the 4-bar evolving on randomly generated trees of 500 taxa. Each point represents variance in the length of the 4-bar links among the 500 tip taxa vs variance in their Maxillary KT. The relationship is significant but weak ($r^2 = 0.25$). Redrawn from data in Alfaro *et al.* (2004).

tions in addition to maxillary rotation and upper jaw protrusion. For example, the mechanisms of buccal expansion, the action that is key to suction feeding, involves oral jaw expansion. Thus, the parts of the 4-bar linkage are simultaneously elements of other linkage systems and participate in other functions. It is therefore of interest to explore the consequences of many-to-one mapping for participation in multiple functions. Consider a second mechanical property of the 4-bar linkage that we will call the Nasal KT. We will define the Nasal KT as output rotation of the nasal bone (Fig. 1) for a given amount of input rotation of the lower jaw. As with Maxillary KT, there is many-to-one mapping of 4-bar shape onto Nasal KT (Fig. 4).

Because many shapes give each value of KT, it is possible to obtain many combinations of Nasal KT and Maxillary KT (Alfaro *et al.*, 2004). Furthermore, there is considerable flexibility for simultaneously optimizing both properties. An example is shown in figure 4 where the intersection between Maxillary KT = 0.8 and Nasal KT = 0.5 is illustrated. The intersection between these two surfaces in 4-bar morphospace defines a family of 4-bar shapes that all have this combination of mechanical properties.

The implications of this phenomenon for the evolution of functional systems are considerable. There are many different mechanical properties of the skull of fishes that involve many different functions. The morphological systems that underlie these mechanical properties will frequently have overlapping parts. If morphological shape mapped one-to-one then every skull shape would map to a unique combination of mechanical properties and systems with overlapping parts would be highly constrained in their evolution. Many-to-one mapping results in a partial decoupling that makes it possible to alter the shape of the 4-bar

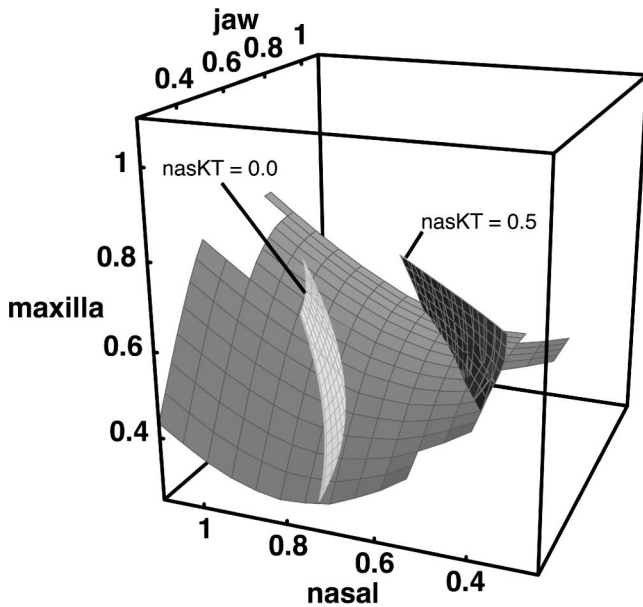


FIG. 4. Three dimensional morphospace of the 4-bar linkage created by expressing each of the three moving links as a fraction of the length of the fixed link. The red surface identifies all 4-bar shapes that have Maxillary KT of 0.8. Shown also are the surfaces for Nasal KT = 0 and Nasal KT = 0.05. The intersection between two surface, such as Maxillary KT = 0.8 and Nasal KT = 0.5 is a line that identifies a family of different shapes that all have these mechanical properties. Figure is redrawn from Alfaro *et al.* (2005).

in order to change one mechanical property, while keeping a second mechanical property constant. This would not be possible if form mapped to mechanical property in a one-to-one fashion.

Have labrid fishes capitalized on this property of the 4-bar linkage? Figure 5A illustrates the 4-bar shapes of six labrid species all with Maxillary KT = 0.8 (± 0.04) and Nasal KT of 0.5 (± 0.04) (Wainwright *et al.*, 2004). Note that the shapes of these six linkages are all different. These species lie at different positions along the line that intersects Maxillary KT = 0.8 and Nasal KT = 0.5. The significance of many-to-one in promoting diversity in this group is further illustrated by the fact that various other species, all with Maxillary KT = 0.8 exhibit a wide range of Nasal KT values (Fig. 5B). The structural complexity of the linkage between lower and upper jaw permits a greater range of mechanical combinations than would be permitted with the simpler underlying system.

As one increases the number of mechanical properties of the 4-bar system being considered to three, the most common result is that a single shape is found at the intersections of the three individual surfaces. In general, once the number of mechanical properties being determined is equal to or greater than the number of underlying links that specify the mechanical property there is usually one or fewer forms that have the combination of properties. In order to see many-to-one mapping in functional systems there have to be more parts interacting to specify the properties than there are emergent properties being evaluated.

A mechanism for strong phylogenetic constraints on form

Since many 4-bar shapes have the same Maxillary KT this creates a question about what happens when convergent evolution occurs in the mechanical property. Does selection for a particular value of Maxillary KT always produce the same morphology as we commonly expect in studies of convergent evolution? Alternatively, many-to-one mapping may make the morphological evolution that accompanies mechanical convergence less predictable. Perhaps the ancestral form of the 4-bar linkage strongly affects the morphological outcome of convergence in Maxillary KT.

To explore these possibilities we simulated the evolution of the 4-bar linkage using an explicit genetic model of 4-bar evolution (Alfaro *et al.*, 2004). To model the genetic basis of the 4 morphological traits, we used an additive multilocus model with uniform allele effects. Every individual was assigned a haploid genotype that determined the lengths of the four links in the 4-bar. The genotype consisted of 50 loci for each of the 4 traits. After assigning each of 500 starting individuals a genotype and phenotype, the population was subjected to natural selection on Maxillary KT through hundreds of generations of reproduction and recombination. We chose three morphologically and mechanically different 4-bar shapes as alternative starting points for simulations. These morphologies were chosen from actual jaw shapes observed in three wrasse species and had Maxillary KT values of 0.68, 0.98, and 1.65. All morphologies were then subjected to convergent selection over 100 generations for an optimal Maxillary KT of 1.0. All populations converged to this value of Maxillary KT, but the resulting morphologies were highly variable with final form depending strongly on the starting shape (Fig. 6). The repeatability with which different starting morphologies evolved to specific regions of morphospace represents a phylogenetic constraint on 4-bar shape. Based on these simulations convergent evolution of 4-bar mechanics would not be expected to produce convergence in morphology.

THE GENERALITY OF MANY-TO-ONE MAPPING

Many-to-one mapping is a ubiquitous feature of biological design. Genetic epistasis produces many-to-one mapping of genotypes to phenotypes and has long been recognized as a basic property of plant and animal genetic systems. Many-to-one mapping occurs between genotype and RNA secondary structure (Fontana and Schuster, 1998; Schuster, 2000). Protein structure maps redundantly onto function (Adinolfi *et al.*, 2002; Hughes, 1994; Kitami and Nadeau, 2002). For many physiological properties of organisms there is redundant mapping of the underlying features to values of the physiological, mechanical or performance property (Koehl, 1996; Kovach, 1996; Nishikawa, 1999; Norberg, 1994; Taylor and Weibel, 1981; Wainwright *et al.*, 1976). For example, at the level of

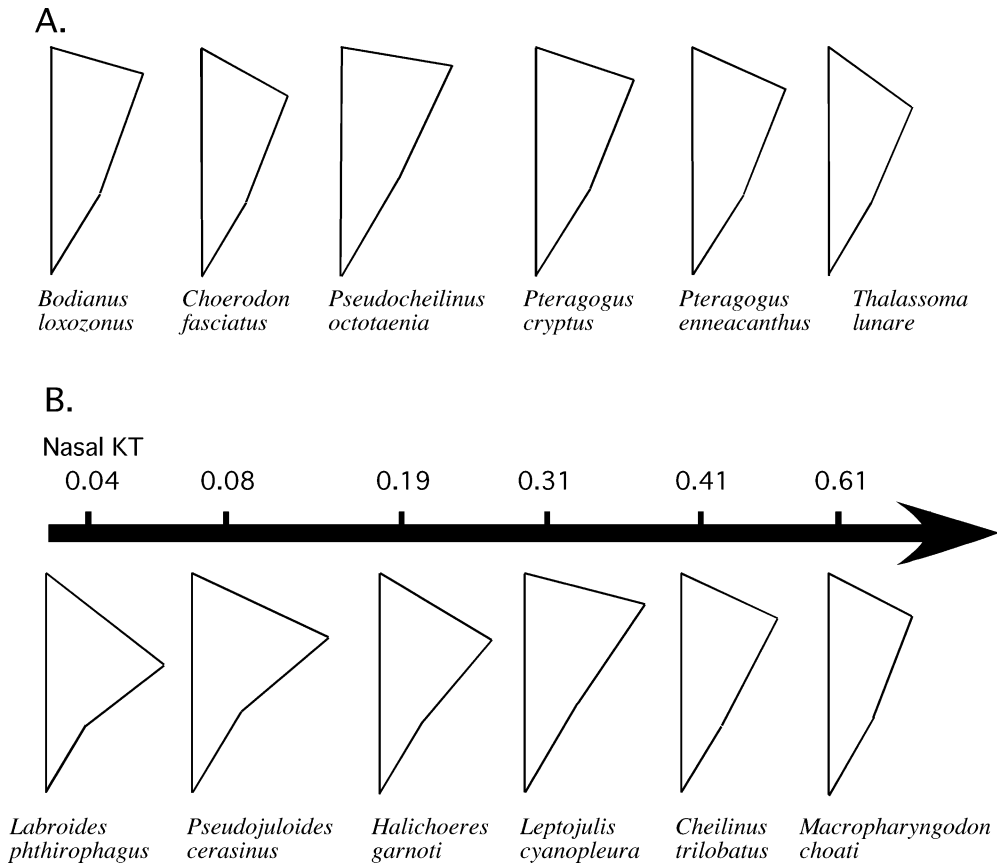


FIG. 5. (A). Examples of six labrid species that share the same values of Maxillary KT (about 0.8) and Nasal KT (about 0.55) in the oral jaw 4-bar linkage. Note that while these mechanical properties are the same, the shapes differ among these species. (B). Six labrid fish species that share the same value of Maxillary KT (about 0.8), but differ in Nasal KT. Figure is redrawn from Alfaro *et al.* (2005).

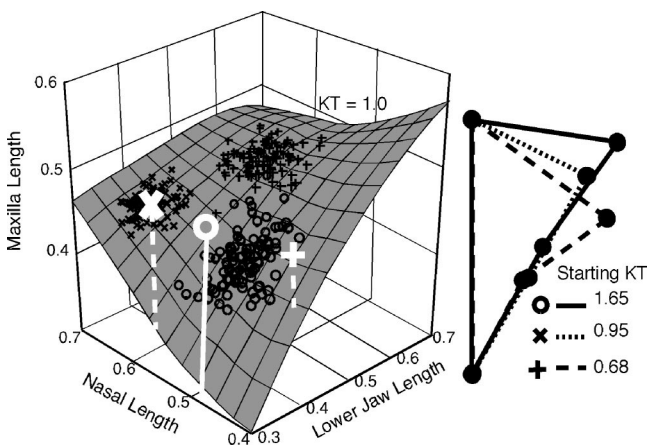


FIG. 6. Plot showing the results of simulations of convergent evolution of three different 4-bar shapes on Maxillary KT = 1.0. Starting morphologies are indicated by white symbols with vertical lines drawn to the x-y plane. Ending morphologies (black symbols) all lie on the KT = 1.0 surface. Despite this functional convergence, ending shape varied considerably and depended on starting morphology. Three randomly selected ending morphologies (with KT = 1.0) are drawn for comparison. Redrawn from data in Alfaro *et al.* (2004).

whole-organism performance, lizards with many different combinations of hind limb dimensions and leg muscles can have the same jumping ability (Toro *et al.*, 2004). A familiar example of many-to-one mapping occurs in vertebrate skeletal muscle where a constant muscle volume can be arranged in many different combinations of specific tension, fiber length and fiber orientation (angle of pennation) to produce muscles with the same tension-producing capacity (Powell *et al.*, 1984). In cases where the emergent property of a system is produced by an interaction of three or more components there is likely to be redundant mapping.

By analogy with the labrid feeding system that we have studied, we expect many-to-one mapping to have several general consequences for the evolution of complex functional systems. First, and this is our major point in this paper, redundant mapping promotes diversity of functional systems in evolving clades of organisms. The presence of surfaces of neutral morphological variation with respect to individual emergent properties, and neutral mechanical variation of one property with respect to another, permit more total combinations of the emergent properties. Many-to-one mapping of 4-bar shape to Maxillary and Nasal KT in labrid fishes means that many more combinations of these mechanical properties are possible than would

be under the more restricted conditions of one-to-one mapping as seen in simpler systems. This is a relatively unexplored consequence of many-to-one mapping but is related to the notion of decoupling that has received considerable attention (Friel and Wainwright, 1998; Lauder, 1990; Liem and Osse, 1975; Schaefer and Lauder, 1986, 1996).

Second, the relationship between diversity that is measured at different levels of design is weakened by many-to-one mapping. Conformation at the lower level precisely determines functional properties at the level above, but the reverse is not true. In the labrid 4-bar case it would not be possible to infer jaw morphology given Maxillary KT. The weak correlations between morphological and mechanical diversity in our simulations that was caused by the many-to-one mapping of 4-bar form to Maxillary KT is, by extension, discouraging for attempts to infer patterns of niche diversity from variation in morphology (Gatz, 1979; Leisler and Winkler, 1991; Lovette *et al.*, 2002; Winemiller, 1991). Previous authors have noted that morphology may not map closely to ecology because of the nature of behavioural or performance filters that are imposed on this relationship (Moreno and Carrascal, 1993; Ricklefs and Miles, 1994). Our observations, like those by Koehl (1996) on the nonlinear mapping of form to mechanics in many systems, provide an intrinsic mechanism in the relationship between form and mechanics that also can weaken this relationship.

Third, redundant mapping provides a clear mechanism for strong phylogenetic effects in the evolution of complex physiological systems. Our simulations of convergent evolution of 4-bar Maxillary KT show that the flexibility in morphological solution for each value of KT means that the path through morphospace that a lineage follows is strongly influenced by the morphology it begins with, as is the ending morphology. This phenomenon, relatively unexplored in the literature, is likely to contribute to overall clade diversity as the walks through morphospace from one value of KT to the next are likely to be unique to each lineage and strongly influenced by history.

The importance of complexity for the evolution of functional diversity has been widely recognized in the literature (Lipson *et al.*, 2002; McShea, 2000; Vermeij, 1973*a, b*) and many-to-one mapping can be thought of as a special case of this general principal. Lineages of organisms that are made of more independently varying parts than other lineages are thought to have the potential to become more morphologically diverse (Vermeij, 1973*a*). An important goal in future research will be to evaluate the importance of redundant mapping in influencing the diversity of functional systems. We suggest that a profitable avenue to pursue will be to identify monophyletic groups that are characterized by novelties that increase the structural complexity of specific systems and generate patterns of many-to-one mapping. Tests can then be constructed to compare the diversity of the functional system in the group pos-

sessing the novelty to that of its sister group or parphyletic outgroup. Such studies will help determine the significance of intrinsic properties of physiological design for the uneven distribution of functional diversity in the tree of life.

ACKNOWLEDGMENTS

We thank Michael Turelli for advice during various phases of this research and the National Science Foundation is gratefully acknowledged for grant support.

REFERENCES

- Adinolfi, S., M. Trifuoggi, A. S. Politou, S. Martin, and A. Pastore. 2002. A structural approach to understanding the iron-binding properties of phylogenetically different frataxins. *Hum. Mol. Gen.* 11:1865–1877.
- Alfaro, M. E., D. I. Bolnick, and P. C. Wainwright. 2004. Evolutionary dynamics of complex biomechanical systems: An example using the four-bar mechanism. *Evolution*. 58:495–503.
- Alfaro, M. E., D. I. Bolnick, and P. C. Wainwright. 2005. Evolutionary consequences of many-to-one mapping of jaw morphology to mechanics in labrid fishes. *Am. Nat.* (In press)
- Anker, G. C. 1974. Morphology and kinematics of the stickleback, *Gasterosteus aculeatus*. *Trans. Zool. Soc. Lond.* 32:311–416.
- Baldwin, B. G. and M. J. Sanderson. 1998. Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proc. Nat. Acad. Sci. U.S.A.* 95:9402–9406.
- Bartholomew, G. A. 1981. A matter of size an examination of endothermy in insects and terrestrial vertebrates. *In* B. Heinrich (ed.), *Insect thermoregulation*, pp. 45–78. John Wiley and Sons, Inc., New York, New York.
- Block, B. A., J. R. Finnerty, A. F. R. Stewart, and J. Kidd. 1993. Evolution of endothermy in fish: Mapping physiological traits on a molecular phylogeny. *Science* 260:210–214.
- De Visser, J. and C. D. N. Barel. 1996. Architectonic constraints on the hyoid's optimal starting position for suction feeding of fish. *J. Morphol.* 228:1–18.
- Farrell, B. D. 1998. "Inordinate fondness" explained: Why are there so many beetles? *Science* 281:555–559.
- Fontana, W. and P. Schuster. 1998. Shaping space: The possible and the attainable in RNA genotype-phenotype mapping. *J. Theor. Biol.* 194:491–515.
- Foote, M. and S. J. Gould. 1992. Cambrian and recent morphological disparity. *Science* 258:1816.
- Friel, J. P. and P. C. Wainwright. 1998. Evolution of motor patterns in tetraodontiform fishes: Does muscle duplication lead to functional diversification? *Br. Behav. Evol.* 52:159–170.
- Gatz, A. J. 1979. Community organization in fishes as indicated by morphological features. *Ecology* 60:711–718.
- Hochachka, P. W. and P. L. Lutz. 2001. Mechanism, origin, and evolution of anoxia tolerance in animals. *Comp. Biochem. Physiol. Part B, Biochem. Mol. Biol.* 130B:435–459.
- Huey, R. B. and A. F. Bennett. 1987. Phylogenetic studies of coadaptation: Preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41:1098–1115.
- Hughes, A. L. 1994. The evolution of functionally novel proteins after gene duplication. *Proc. Roy. Soc. Lond., Ser. B. Biol. Sci.* 256:119–124.
- Hulse, C. D. and P. C. Wainwright. 2002. Projecting mechanics into morphospace: Disparity in the feeding system of labrid fishes. *Proc. Roy. Soc. Lond., Ser. B. Biol. Sci.* 269:317–326.
- Kitami, T. and J. H. Nadeau. 2002. Biochemical networking contributes more to genetic buffering in human and mouse metabolic pathways than does gene duplication. *Nat. Genet.* 32:191–194.
- Koehl, M. A. R. 1996. When does morphology matter? *Annu. Rev. Ecol. Syst.* 1996:501–542.
- Kovach, I. S. 1996. A molecular theory of cartilage viscoelasticity. *Biophys. Chem.* 59:61–73.

- Lauder, G. V. 1981. Form and function: Structural analysis in evolutionary morphology. *Paleobiology* 7:430–442.
- Lauder, G. V. 1990. Functional morphology and systematics: Studying functional patterns in an historical context. *Annu. Rev. Ecol. Syst.* 21:317–340.
- Leisler, B. and H. Winkler. 1991. Results and concepts in the ecomorphology of birds. *J. Fuer Ornith.* 132:373–426.
- Liem, K. F. and J. W. M. Osse. 1975. Biological versatility, evolution, and food resource exploitation in African cichlid fishes. *Amer. Zool.* 15:427–454.
- Lipson, H., J. B. Pollack, and N. P. Suh. 2002. On the origin of modular variation. *Evolution* 56:1549–1556.
- Lovette, I. J., E. Bermingham, and R. E. Ricklefs. 2002. Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. *Proc. Roy Soc. Lond., Ser. B: Biol. Sci.* 269:37–42.
- McShea, D. W. 2000. Functional complexity in organisms: Parts as proxies. *Biol. Phil.* 15:641–668.
- Middleton, K. M. and S. M. Gatesy. 2000. Theropod forelimb design and evolution. *Zool. J. Linn. Soc.* 128:149–187.
- Moreno, E. and L. M. Carrascal. 1993. Leg morphology and feeding postures in four *Parus* species: An experimental ecomorphological approach. *Ecology* 74:2037–2044.
- Nishikawa, K. C. 1999. Neuromuscular control of prey capture in frogs. *Phil. Trans. Roy. Soc. Lond. B Biol. Sci.* 354:941–954.
- Norberg, U. M. 1994. Wing design, flight performance, and habitat use in bats. *In* P. C. Wainwright and S. M. Reilly (eds.), *Ecological morphology*, pp. 205–239. University of Chicago Press, Chicago.
- Norberg, U. M. 2002. Structure, form, and function of flight in engineering and the living world. *J. Morphol.* 252:52–81.
- Ostrom, J. H. 1979. Bird flight: How did it begin? *Amer. Sci.* 67: 45–56.
- Powell, P., R. R. Roy, P. Kanim, M. A. Bello, and V. Edgerton. 1984. Predictability of muscle tension from architectural determinations in guinea pig hindlimbs. *J. Appl. Physiol.* 57:1715–1721.
- Ricklefs, R. E. and D. B. Miles. 1994. Ecological and evolutionary inferences from morphology: An ecological perspective. *In* P. C. Wainwright and S. M. Reilly (eds.), *Ecological morphology*, pp. 13–41. University of Chicago Press, Chicago.
- Schaefer, S. A. and G. V. Lauder. 1986. Historical transformation of functional design: Evolutionary morphology of the feeding mechanisms of loricatorid catfishes. *Sys. Zool.* 35:489–508.
- Schaefer, S. A. and G. V. Lauder. 1996. Testing historical hypotheses of morphological change: Biomechanical decoupling in loricatorid catfishes. *Evolution* 50:1661–1675.
- Schuster, P. 2000. Taming combinatorial explosion. *Proc. Nat. Acad. Sci. U.S.A.* 97:7678–7680.
- Streelman, J. T., J. F. Webb, R. C. Albertson, and T. D. Kocher. 2003. The cusp of evolution: A model of cichlid tooth shape diversity. *Evol. Devel.* 5:600–608.
- Taylor, C. R. and E. R. Weibel. 1981. Design of the mammalian respiratory system. I. Problem and strategy. *Respir. Physiol.* 44: 1–10.
- Toro, E., A. Herrel, and D. Irschick. 2004. The evolution of jumping performance in Caribbean *Anolis* lizards. *Amer. Natur.* 163: 844–856.
- Vermeij, G. 1973a. Adaptation, versatility and evolution. *Sys. Zool.* 22:466–477.
- Vermeij, G. 1973b. Biological versatility and earth history. *Proc. Nat. Acad. Sci. U.S.A.* 70:1936–1938.
- Wainwright, P. C., D. R. Bellwood, M. W. Westneat, J. R. Grubich, and A. Hoey. 2004. A function morphospace for the skull of labrid fishes: Patterns of diversity in a complex biomechanical system. *Biol. J. Linn. Soc.* 82:1–25.
- Wainwright, S. A., W. D. Biggs, J. D. Curry, and J. M. Gosline. 1976. *Mechanical design in organisms*. Edward Arnold, London.
- Wake, D. B. 1982. Functional and evolutionary morphology. *Pers. Biol. Med.* 25:603–620.
- Westneat, M. W. 1990. Feeding mechanics of teleost fishes (Labridae, Perciformes)—a test of 4-bar linkage models. *J. Morphol.* 205:269–295.
- Westneat, M. W. 1995. Feeding, function and phylogeny: Analysis of historical biomechanics in labrid fishes using comparative methods. *Syst. Biol.* 44:361–383.
- Winemiller, K. O. 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecol. Monogr.* 61:343–365.