Chapter Nine

How Does Morphology Affect Performance in Variable Environments?

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The preceding chapters in the section on "Mechanisms, molecules, and evo-devo" deal with the genetic and developmental mechanisms that produce and limit phenotypic diversity and morphological changes as lineages of organisms evolve. To understand the selective consequences of such phenotypic variations, we also need to determine whether or not morphological differences between organisms affect their relative performance in natural environments, as well as how those effects depend on the habitat. Studies of the physiology and biomechanics of organisms are useful tools in assessing the functional consequences of phenotypic differences. The purpose of this chapter is to explore some of the ways in which the performance consequences of differences in morphology are affected by the environment in which an organism lives.

BACKGROUND

The relationship between the form and function of organisms has long been studied (e.g., reviewed in Koehl 1996). One approach to investigating functional morphology is biomechanics, which applies quantitative engineering techniques to study how organisms perform mechanical functions and interact with their physical environments. By elucidating basic physical rules governing how biological structures operate, biomechanical studies can identify which structural characteristics affect the performance of a defined function and can analyze

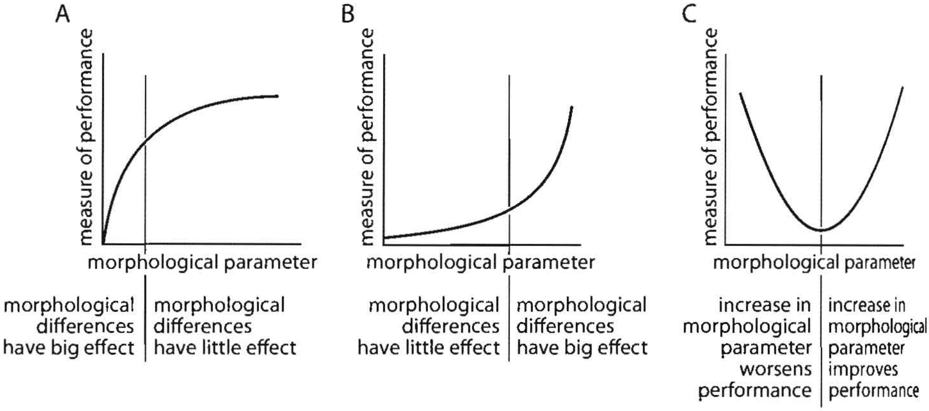

Figure 9.1. Examples of nonlinear ways in which a measured aspect of performance can vary as a function of a quantified morphological parameter. Biological examples of each of these types of curves are reviewed by Koehl (1996).

the mechanisms responsible for the effects of morphological differences on performance.

Biomechanical analyses have revealed that the dependence of measures of performance on quantifiable aspects of morphology is often nonlinear (reviewed by Koehl 1996, 2000). When the effect of morphology on performance is nonlinear, there are ranges of the morphological parameter in which changes in structure have little effect on function, and other ranges where small morphological modifications can have large consequences. For example, if an asymptotic curve describes the dependence of performance on a morphological parameter, then changes in that parameter at low values can have a big effect on performance, whereas changes in that parameter at high values can make little difference to function (fig. 9.1a). Conversely, if an exponential curve describes how function depends on structure, then performance should be insensitive to structural variation at small values of the morphological parameter, but be very sensitive to morphological changes at large values of the parameter (fig. 9.1b). In the range where morphology has little effect on the performance of a particular function, there can be permission for morphological diversity without consequences for that function. Furthermore, selection on that morphological variable based on performance of a different task can occur without jeopardizing the performance of the first function. If the relationship between performance and a morphological variable goes through a maximum or a minimum (fig. 9.1c), then the effect of increasing the morphological variable reverses once it passes a critical value. Passing through such an inflection point represents the acquisition of a novel consequence for a particular type of morphological change. In addition to the examples of nonlinear relationships between morphology and performance illustrated in figure 9.1, some mechanical behaviors (such as buckling under a load) and fluid dynamic processes (such as the transition to turbulence) are unaffected by morphological variations except in a critical range, where a small change in size or shape causes a sudden, drastic switch in performance.

The influence of environmental variables on how morphology affects function can also be nonlinear and can lead to surprising relationships between phenotype and performance. In this chapter, I present some examples from my work and that of my students that illustrate how the consequences of morphological differences can depend on the location of organisms within a habitat, and on the timing of organism behaviors and life history stages relative to temporal changes in the environment.

CONSEQUENCES OF MORPHOLOGICAL DIFFERENCES CAN DEPEND ON THE ENVIRONMENT

Does Morphology Matter? (Habitat affects whether or not morphology affects performance)

Many bottom-dwelling marine organisms produce microscopic larvae that are dispersed by ocean currents, and then settle back onto the substratum and metamorphose into benthic juveniles. These larvae and juveniles provide an example of how habitat can determine whether or not morphology affects performance. For a larva to recruit to a benthic habitat that is exposed to ambient water flow, it must not wash away during settlement and metamorphosis. Drag is the hydrodynamic force acting in the same direction as the ambient water flow that pushes the larva downstream. Most larvae of benthic marine invertebrates are very small (a few hundred microns). How do the changes in body shape that occur during metamorphosis affect the drag experienced by a larva versus a newly metamorphosed juvenile sitting on a substratum in the ocean?

We are addressing this question using the sea slug, *Phestilla sibogae*, which is an important model organism for studying larval settlement.

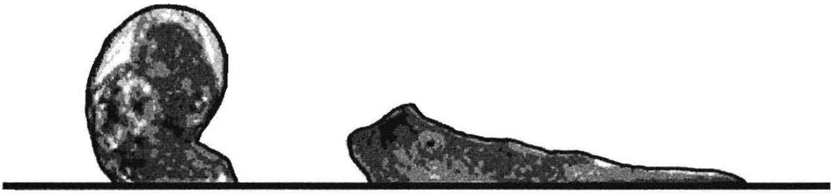

Figure 9.2. Diagram of a lateral view of the body shape of a newly settled larva, and of a newly metamorphosed juvenile of the sea slug, *Phestilla sibogae*. The anterior end of each animal is to the left.

A larva of *P. sibogae* settles onto the substratum (fig. 9.2) and then undergoes metamorphosis into a juvenile benthic slug (details in Bonar and Hadfield 1974). *P. sibogae* slugs live on coral reefs dominated by their prey, the branching coral, *Porites compressa*. Coral reefs are porous, so there are surfaces on which larvae can land inside the reef as well as on the top of the reef. *P. compressa* reefs are exposed to turbulent, wave-driven water flow with peak freestream velocities of ~0.4 m/s, and to much slower flow (peak velocities of ~0.04 m/s) through the spaces within the porous reef (Koehl and Hadfield 2004). When fluid flows over a solid surface, a boundary layer of slowed fluid develops along the surface (e.g., Vogel 1994; Koehl 2007). Therefore, to determine the drag that could wash settled larvae and juveniles off a reef, we need to know the water velocities encountered by organisms only 200 μm tall sitting on surfaces of the reef. We used laser-Doppler velocimetry to measure water velocities 200 μm from coral surfaces at the top of a reef (velocity peaks of 0.085 m/s) and at various positions down within a reef (e.g., 0.007 m/s at 200 μm from surfaces 10 cm below the top of the reef) (Reidenbach et al. 2008).

Measuring the drag on larvae and juveniles of *P. sibogae* is challenging because they are so small. We met this challenge by borrowing a technique routinely used by engineers to study fluid dynamic forces on objects of inconvenient sizes: dynamically scaled physical modeling. If a model is scaled dynamically, then the ratios of the forces and of the velocities in the fluid around a model are the same as those for comparable positions around the real larva, and fluid dynamic forces measured on the model can be used to calculate the forces on the real animal (e.g., Koehl 2003). Reynolds number (Re) is the ratio of inertial forces to viscous forces for a particular flow situation ($Re = LU\rho/\mu$, where L is a linear dimension of the body, U is the velocity of the fluid relative to the body, ρ is the density of the fluid, and μm is the dynamic viscosity of the fluid, which is its resistance to being sheared) (e.g., Vogel 1994). If the Re of a model and the Re of its prototype organism are the same, then the model is dynamically similar to the organism. We made big models (L ~ 5 cm) of microscopic larvae and juveniles, but we kept the Re's of the models the same as the Re's of the larvae and juveniles by lowering the velocity of the fluid relative to the models, and by using a fluid (mineral oil) with a higher viscosity than that of water.

We used these dynamically scaled physical models to determine the hydrodynamic forces on larvae and on newly metamorphosed juveniles of *P. sibogae* sitting on solid surfaces at different positions on a coral reef (Kreft, Waldrop, and Koehl unpublished data). Surprisingly, when exposed to flow at Re = 2 (like they experience within the reef), there was no significant difference between the drag on the upright, bulbous larva and the sleek, flat juvenile (drag on both shapes was ~10 nN). Body shape did *not* affect hydrodynamic performance of these small animals in within-reef microhabitats. In contrast, when exposed to flow at Re = 17 (like they experience at the top of a coral reef), body shape had a big effect on hydrodynamic performance: drag on the larva (~240 nN) was nearly three times greater than drag on the juvenile (~90 nN).

How can shape affect drag on organisms in one region of a habitat, but not in another? The mechanisms responsible for drag depend on the Reynolds number, and hence on the fluid velocity relative to an organism. The Re's of the tiny *P. sibogae* larvae and newly metamorphosed juveniles fall in a very interesting transitional Re range where both viscous and inertial forces are important. At low Re (slow flow), drag is due to "skin friction" (fluid is sheared as it flows across a body, and the viscous resistance of the fluid to being sheared drags the body downstream). At high Re (fast flow), in addition to skin friction, bodies also experience "form drag" (a wake forms on the downstream side of a body, and the resulting pressure difference between the upstream and downstream sides of the body push it downstream) (e.g., details in Vogel 1994). Bluff bodies that produce wide wakes experience higher form drag than streamlined shapes that have narrow wakes. By measuring the fluid velocity fields around our models (Kreft, Waldrop, and

Koehl unpublished data), we discovered that wakes formed at the higher Re of larvae and juveniles at the top of the reef (accounting for about 90% of the drag on the bluff larva, but only about 35% of the drag on the streamlined juvenile), hence body shape affected drag. In contrast, at the lower Re they experience within the reef, form drag and body shape were not important.

Comparison of hydrodynamic forces with the attachment strengths of larvae and juveniles of *P. sibogae* (Koehl and Hadfield 2004) indicates that larvae have a high probability of washing away at the top of the reef but not within it (Reidenbach et al. 2008), suggesting that larval settlement occurs within the reef. In contrast, if the juveniles crawl up to the top of the reef where the living coral tissue on which they feed is most abundant, they are unlikely to be swept away.

This example focuses on an ontogenetic transformation in morphology rather than an evolutionary change in form. Nonetheless, it illustrates a general principle for small organisms operating at these intermediate Re's: differences in the water current or wind velocity that occur within a spatially diverse environment can determine whether or not form drag, and hence body shape, affects the fluid dynamic performance of the organisms.

Does a Morphological Change Improve or Worsen Performance? (Habitat effects on the consequences of a morphological change)

Not only do bottom-dwelling aquatic organisms have to withstand the forces imposed on them by ambient water flow, but they also can use that water motion for the transport of materials. For example, moving water supplies oxygen to benthic organisms, dissolved nutrients to algae, and planktonic food to suspension feeders. Ambient currents also carry away wastes released by organisms and can disperse their gametes, spores, or larvae. We have been investigating ways in which the morphology of benthic organisms affects their performance in utilizing ambient water motion for transport. Several of those studies have revealed examples of how the habitat determines whether a specific change in morphology improves or worsens performance.

Bryozoans, colonial animals that live attached to surfaces in aquatic environments, are suspension feeders that capture planktonic prey from the water flowing past them. For upright arborescent colonies, habitat determines the effect of colony size on the feeding rates of the zooids in the colony (Okamura 1984). An increase in colony size can lead to a decrease in the rate of capture of food particles per zooid in habitats characterized by slow ambient currents because the upstream zooids in a colony deplete the water of planktonic food particles. In contrast, in habitats exposed to rapidly flowing water, colony size has the opposite effect on feeding rate per zooid. If the ambient water current is too fast, zooids cannot hold on to prey particles. As water flows between the branches of a large colony, it is slowed more than it is by a small colony. Therefore, zooids in a large colony are able to catch and retain food particles in ambient water currents that are so fast that zooids in small colonies cannot feed.

Habitat can also determine the effect of morphology on the dispersal of materials (e.g., wastes, gametes) released by bottom-dwelling aquatic organisms. We used physical models of benthic animals of different sizes (1–10 cm in height) to investigate how body size affects the dispersal of materials they shed. The models were affixed to a wave-swept rocky shore, either on bare rock or surrounded by a canopy of models of flexible seaweeds (~50 cm long). Each model animal released dye (an analogue for water-borne substances released by benthic animals) from an opening at its top, and the dispersal of the dye in the ambient water flow was measured as a function of time (techniques described in Koehl et al. 1993). We found that the effect of the height of a model animal on the dispersal of material it released into wave-driven flow depended on its neighbors. Size had no effect on dispersal from solitary model animals on wave-swept rocks. In contrast, height had a surprising effect on dispersal of dye released by the same model animals when surrounded by canopies of flexible model seaweeds: dispersal was faster for short organisms than for tall ones. The mechanism responsible for this effect is that waves whiplash flexible macroalgae back and forth near the substratum (Koehl 1999). The flailing fronds stirred the water down near the rock surface, thereby spreading material released by short organisms more quickly than material released by organisms that stood taller than the whiplashing seaweeds (Koehl and Powell unpublished data).

These examples of mass exchange between benthic organisms and the surrounding water illustrate that both the abiotic and biotic

Figure 9.3. Diagram of a dorsal view of a basal non-flying frog and a derived "flying" frog (redrawn from Emerson and Koehl 1990). The hands, feet, and skin flaps are shown in stippled light gray. Both flyers and non-flyers assume the posture shown in these diagrams when they fall through the air (McCay 2001b).

environments of organisms can alter how differences in morphology affect performance.

Which Function Is Important? (Habitat use in spatially complex, temporally varying environments)

We have been using tree frogs in tropical rain forests to study the evolution of a novel mode of locomotion: gliding. In two separate lineages, the Hylidae and the Rhacophoridae, "flying" frogs that glide through the air have evolved. In both clades, the derived "flying" species have enlarged, highly webbed hands and feet and skin flaps on arms and legs, whereas the more basal species do not (Emerson and Koehl 1990; McCay 2001a). We studied aerodynamic behavior of "flyers" and non-flyers in the field (Emerson and Koehl 1990) and in a wind tunnel (McCay 2001a), and used those data to design wind tunnel experiments in which the aerodynamic forces on physical models of the frogs were measured. The models enabled us to vary one or more morphological or postural features at a time to quantify the effects of each; thus we could determine the aerodynamic consequences of the "flying" morphology (Emerson and Koehl 1990; McCay 2001a, 2001b).

The distinctive morphological features of gliding animals traditionally have been evaluated by their effects on glide performance, the horizontal distance traveled per vertical distance fallen, which is equal to the ratio of lift (the force perpendicular to the direction of air flow relative to the body) to drag (the force parallel to the air flow direction relative to the body) (e.g., Vogel 1994). Surprisingly, our experiments revealed that the lift-to-drag ratio was lower (i.e., gliding performance was worse) for "flying" frogs than for non-flyers (Emerson and Koehl 1990; McCay 2001b). However, consideration of how frogs locomote through the air in rain forests suggests that glide performance is not the aspect of aerodynamic function that is most likely to affect fitness.

Airborne frogs maneuver through complex plant canopies to reach breeding pools on the forest floor (e.g., McCay 2001), so we studied how the morphological features of "flying" frogs affected their stability in the face of ambient wind gusts, and their maneuverability in steering their way through the trees. A stable aircraft passively rights itself after being perturbed (for example, by a wind gust), a neutrally stable aircraft does not right itself, and an unstable one continues to tumble passively after the perturbing force has ceased. If a frog falling through the air has an aerodynamically stable shape, then its body passively resists maneuvers that the frog tries to impose on its trajectory by a steering movement. In contrast, a neutrally stable shape does not fight maneuvers, and an unstable shape enhances them. Thus, there is a trade-off between aerodynamic stability and maneuverability. Our model studies showed that the non-flyer tree frogs are aerodynamically stable, but the "flying" frogs are unstable in pitch (rotating nose up or down) and yaw (turning right or left) (Emerson and Koehl 1990; McCay 2001b). McCay's (2001a) wind tunnel studies with living frogs showed that they turn by changing the angles of their feet. Using physical models in the wind tunnel, he measured the moments generated by changing the angle of one foot by frogs of different morphologies and found that "flying" frogs have higher "control effectiveness" than do non-flyers (i.e., they generate bigger moments per foot angle change) (McCay 2001b). Since "flying" frogs are also unstable, they do not offer passive resistance to a moment generated by a foot. Together, these two features make them more "agile" (i.e., they can turn more rapidly for a given change in foot angle) than non-flyer frogs.

Our aerodynamic experiments showed that non-flyer tree frogs are stable and passively right themselves if perturbed by a wind gust, whereas "flying" frogs are unstable, but maneuverable. Do those different attributes affect their parachuting performance under natural wind conditions in a rain forest? McCay (2003) measured wind speeds and turbulent velocity fluctuations at a range of heights in a rainforest canopy at different times during the day and night. He found that daytime winds could be gusty. However, the frogs only glided at night, when the air was generally quite still (average velocities only ~0.01 m/s). Therefore, the danger of an unstable "flying" frog being tumbled by a wind gust is low during the times that the frogs are gliding in the forest.

The example of "flying" frogs illustrates that we can be easily misled about the consequences of morphological differences if the physical structure of the habitat is not considered, and if the temporal patterns of activity by the animals in nature are not known. In complex forest habitats, maneuverability (rather than glide distance) can be the aspect of aerodynamic performance that has the biggest effect on fitness, and the aerodynamic instability that contributes to maneuverability may not pose problems if the animals do not glide during times of day when the wind is gusty.

What Is "Good" Performance? (Ontogenetic changes in the function of a structure in the environment)

Biomechanical investigations sometimes reveal that the morphologies of organisms result in "bad" mechanical performance such as breakage, but field studies of the ways those organisms function in their environments at different stages in their lives can help us understand how such creatures with poor mechanical performance can survive and reproduce. Attached marine organisms (e.g., seaweeds, corals) provide a number of examples of how seemingly "bad" engineering designs can sometimes enhance the ecological performance of organisms (Koehl 1999).

The tropical seaweed *Turbinaria ornata* provides an example of how ontogenetic changes in morphology cause a significant deterioration in mechanical performance (Stewart 2006). An individual *T. ornata* has fleshy blades attached by a stem-like stipe to a holdfast that adheres to the substratum (fig. 9.4). As a *T. ornata* grows larger and ages, gamete-producing reproductive receptacles develop on the blades and the percent of its body mass devoted to reproductive tissue increases (from 0% up to ~25%). As an individual grows, the drag force due to ambient water currents also increases two- to threefold. *T. ornata* blades can develop gas-filled spaces, and the net buoyant force exerted by a plant

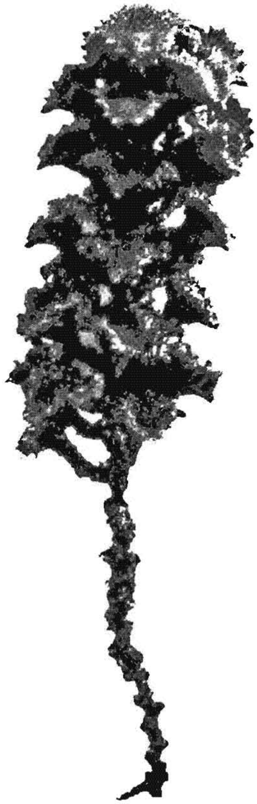

Figure 9.4. Diagram of the alga, *Turbinaria ornata*. Each fleshy blade can contain a buoyant gas-filled compartment and can support a gamete-bearing reproductive receptacle. The blades are connected by the stipe to a holdfast, which is attached to the substratum.

due to these floats changes with age as well: young juveniles are negatively buoyant (net buoyant force of about −0.02N), and older individuals float (net buoyant force of about +0.06N). Since the drag and net buoyant force rise as reproductive effort increases, we might expect the stipe to become wider and stronger as *T. ornata* grow and age. Instead, we find that stipe strength decreases as reproductive effort increases, from ~8 MN.m^2 in juveniles to ~3 MN/m^2 in the most reproductive individuals (strength is the stress required to break stipe tissue, where stress is force per cross-sectional area of tissue bearing that force).

Ambient forces on sessile organisms (e.g., plants, attached aquatic animals) often vary with season, and behaviors of motile animals (e.g., foraging, predator avoidance, migration, social interactions, and fighting) often change with age; thus we use "environmental stress factor" (ESF) to relate the ability of organisms at their particular stages in ontogeny to resist breakage relative to the maximum loads that they experience in nature at those stages (Johnson and Koehl 1994). The ESF for a *T. ornata* is simply an age- and season-dependent safety factor for the stipe (i.e., the ratio of the stress required to break the stipe to the stress in the stipe due to drag imposed by ambient water currents). If ESF ≤ 1, then an individual breaks and washes away. The ambient current velocity at which ESF $= 1$ for juvenile *T. ornata* is 3 m/s, whereas for older reproductive individuals, it is only 1 m/s. Thus, from an engineering point of view, reproductive *T. ornata* have a "bad" morphology and are likely to wash away. However, when the weak, buoyant reproductive individuals break, they float to the water surface where they form rafts with many other reproductive *T. ornata*. The potential for sexual reproduction in these rafts is enhanced, as is long-distance dispersal by ocean currents (Stewart 2006), thus a mechanically "bad" mechanical structure leads to "good" ecological performance that can improve fitness.

T. ornata illustrate that the roles organisms play in their environments at different stages in their ontogeny can determine whether the performance consequences of particular differences in morphology enhance or hurt fitness.

CONCLUSIONS

To understand the consequences of phenotypic variation, we must determine *if* and *how* morphological differences between organisms affect their relative performance in natural environments. The purpose of this chapter has been to explore ways in which the performance consequences of changes in morphology are affected by the environment in which organisms live. The influence of environmental variables on how differences in phenotype affect function can be nonlinear and can lead to surprising relationships between morphology and performance. The example of settling marine larvae illustrated that the environment can determine *whether or not* particular morphological differences affect performance. The studies of suspension feeding and of waste dispersal by benthic marine organisms showed how the neighborhood of an organism can determine if a specific change in structure *improves or worsens performance*. The investigations of flying frogs illustrated that environmental conditions can determine *which aspects of performance are important* to the success of particular organisms. Research on breakable algae provided an example of how a change in *performance can either enhance or hurt ecological success*, depending on the ontogenetic stage of an organism. In sum, these examples show how the effects of different morphologies on performance depend both on the location of organisms within a habitat, and on the timing of organism behaviors and life history stages relative to temporal changes in the environment.

Environmental conditions can affect the performance consequences of different morphologies in surprising ways. Therefore, it can be all too easy, in the absence of field data, to reach the wrong conclusions about how phenotypic differences between organisms might affect their ecological performance or fitness. Since natural environments vary spatially, it is important to determine what conditions are like in the microhabitats experienced by the organisms in question. Furthermore, because environmental conditions vary with time (e.g., diurnally, seasonally), the timing of specific behaviors as well as ontogenetic changes in the ecological roles of organisms need to be determined relative to the temporal fluctuations in their habitats. Therefore, quantitative field studies of where, when, and how organisms with different phenotypes function in their natural habitats can make important contributions to our understanding of the process of morphological evolution.

The work of the Grants provides many examples of the importance of field work to understanding the process of evolution (e.g., Grant 1999). For instance, they coupled analyses of how beak size and musculature determine the size of seeds that a finch can crack with field data on how climatic variation affects seed supply. Their information about food conditions in the field has led to insights about the composition of finch populations with respect to beak morphology, and also about the role of hybrids with intermediate beak sizes in the evolution of sympatric species of finches (Grant and Grant 2006, 2008).

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