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Thrash, Flip, or Jump: The Behavioral and Functional Continuum of Terrestrial Locomotion in Teleost Fishes

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Synopsis Moving on land versus in water imposes dramatically different requirements on the musculoskeletal system. Although many limbed vertebrates, such as salamanders and prehistoric tetrapodomorphs, have an axial system specialized for aquatic locomotion and an appendicular system adapted for terrestrial locomotion, diverse extant teleosts use the axial musculoskeletal system (body plus caudal fin) to move in these two physically disparate environments. In fact, teleost fishes living at the water's edge demonstrate diversity in natural history that is reflected in a variety of terrestrial behaviors: (1) species that have only incidental contact with land (such as largemouth bass, *Micropterus*) will repeatedly thrash, which can roll an individual downhill, but cannot produce effective overland movements, (2) species that have occasional contact with land (like *Gambusia*, the mosquitofish, which evade predators by stranding themselves) will produce directed terrestrial movement via a tail-flip jump, and (3) species that spend more than half of their lives on land (like the mudskipper, *Periopthalmus*) will produce a prone-jump, a behavior that allows the fish to anticipate where it will land at the end of the flight phase. Both tail-flip and prone jumps are characterized by a two-phase movement consisting of body flexion followed by extension—a movement pattern that is markedly similar to the aquatic fast-start. Convergence in kinematic pattern between effective terrestrial behaviors and aquatic fast starts suggests that jumps are an exaptation of a neuromuscular system that powers unsteady escape behaviors in the water. Despite such evidence that terrestrial behaviors evolved from an ancestral behavior that is ubiquitous among teleosts, some teleosts are unable to move effectively on land—possibly due to morphological trade-offs, wherein specialization for one environment comes at a cost to performance in the other. Indeed, upon emergence onto land, gravity places an increased mechanical load on the body, which may limit the maximum size of fish that can produce terrestrial locomotion via jumping. In addition, effective terrestrial locomotor performance may require a restructuring of the musculoskeletal system that directly conflicts with the low-drag, fusiform body shape that enhances steady swimming performance. Such biomechanical trade-offs may constrain which teleost species are able to make the evolutionary transition to life on land. Here, we synthesize the current knowledge of intermittent terrestrial locomotion in teleosts and demonstrate that extant fishes represent an important model system for elucidating fundamental evolutionary mechanisms and defining the physiological constraints that must be overcome to permit life in both the aquatic and terrestrial realms.

Background

Despite evolutionary forces that undoubtedly have selected the teleost body shape for enhanced swimming performance over the past 350 million years, more than 25 teleost genera from diverse taxa spend some portion of their lives on land (Sayer and Davenport 1991). In addition, because the majority of teleost species inhabit shallow, littoral (i.e., near-shore) environments (Carrete Vega and Wiens 2012), individuals from many fully aquatic species often find themselves on land, through either purposeful or accidental stranding. However, all emergent teleosts must return to the water to avoid desiccation and to reproduce—thus, for a surprisingly large number of fishes, the ability to produce goal-directed movements on land is critical for survival. Yet, remarkably little is known about how these fishes move on land.

Because of the different requirements for supporting the body and for generating propulsive forces, being able to move effectively both under water and on land represents a significant functional challenge. One evolutionary "solution" to this problem is modularity (Gatsey and Dial 1996; Clune et al. 2013), that is, the partitioning of tasks to different components of the musculoskeletal system. Indeed, our modern understanding of the origin of early "tetrapodomorphs" is that these tetrapod precursors were able to move onto land because limbs that originally produced movement across an aquatic substrate (Clack 2009; King et al. 2011) eventually enabled the functional partitioning of the axial and appendicular systems—such that limbs were used as the primary locomotor appendages on land and the axial body plus tailfin were used in the water, much as modern salamanders do today (Duellman and Trueb 1994). In contrast, whereas all teleosts retain some ability to move in water—although the degree of aquatic performance may vary—some will occasionally, or even frequently, emerge onto land. Hence, the teleosts that venture onto land are faced with the problem of maintaining locomotor performance in one environment (the water), while also acquiring the ability to move about in a novel environment (on land), in the absence of the limbs and girdles (or analogous structures) that facilitated the movement of the tetrapodomorphs onto land. Indeed, a variety of diverse teleost species appear to be compelled to use the axial musculoskeletal system (body plus caudal fin) to move both in water and on land—that is, for a variety of swimming behaviors and fast start escape responses in water, as well as for terrestrial movements. Given the drastically different physical demands of terrestrial and aquatic environments (e.g., density, viscosity, drag, and acceleration reaction), it would be surprising if the same anatomy and motor control programs that drive swimming or escape behaviors can also produce effective movements on land.

Therefore, a fundamental objective of our research programs, and this paper, is to unravel the evolutionary pathways that result in new behavioral solutions when animals are confronted with a novel environment. Within this conceptual framework, we pose and begin to answer a suite of inter-related questions regarding how teleost fishes cope when confronted with the novel and physically challenging terrestrial environment. (1) What behaviors do teleosts with diverse natural histories use to move about on land? (2) How do new behaviors evolve? (3) Are there intrinsic performance trade-offs between terrestrial and aquatic locomotor behaviors?

Behavior and biomechanics of terrestrial locomotion in teleosts with diverse natural histories

Among extant teleosts, littoral species can be categorized along a continuum. At one end are species like largemouth bass, *Micropterus salmoides*, that have only incidental contact with land; at the other are terrestrial specialists, such as mudskippers (*Periopthalmus*) and amphibious blennies (*Alticus*). The behavior on land of such exemplar species is strikingly different, yet it appears that a variety of species representing phylogenetically and ecologically diverse lineages all are capable of producing locomotor behaviors on land using the axial body plus caudal fin (Fig. 1).

Incidental emersion: thrashing

Individuals of littoral species may find themselves stranded on land for a variety of reasons, including attempting to evade predators (Bayliss 1982), endeavoring to feed on terrestrial prey items located at the water's edge (Kushner et al. 2009; Cucherousset et al. 2012; Pronko et al. 2013), or being propelled by strong currents or flooding onto an exposed bank (Meek 1896). Fish with no evident morphological modifications for terrestrial movement typically produce what appears to the naked eye to be a chaotic and uncoordinated response—this has generated the common metaphor, "a fish out of water," for being out of one's natural element. High-speed image analysis reveals that, when stranded on a flat surface (0° grade), juvenile (4–10 cm total length) largemouth bass respond by producing a series of side-to-side axial muscle contractions we term thrashing (Fig. 2A). This behavior may eventually serve to lift the fish off the substrate, but is relatively ineffective in moving the fish away from the starting position (Fig. 3). Thus, because it is produced via a variable behavior with an inconsistent and unpredictable outcome, it cannot be considered a true jump. However, when stranded on a slope (in the laboratory, fish are placed on a 30° grade covered with dampened sand), thrashing will quickly move a largemouth bass (or other littoral teleost) downslope because axial body movements destabilize the center of mass (COM) and allow gravity to propel the fish downhill (Fig. 4). Depending on the grade, a single thrash or repeated thrashes will enable a fish to roll

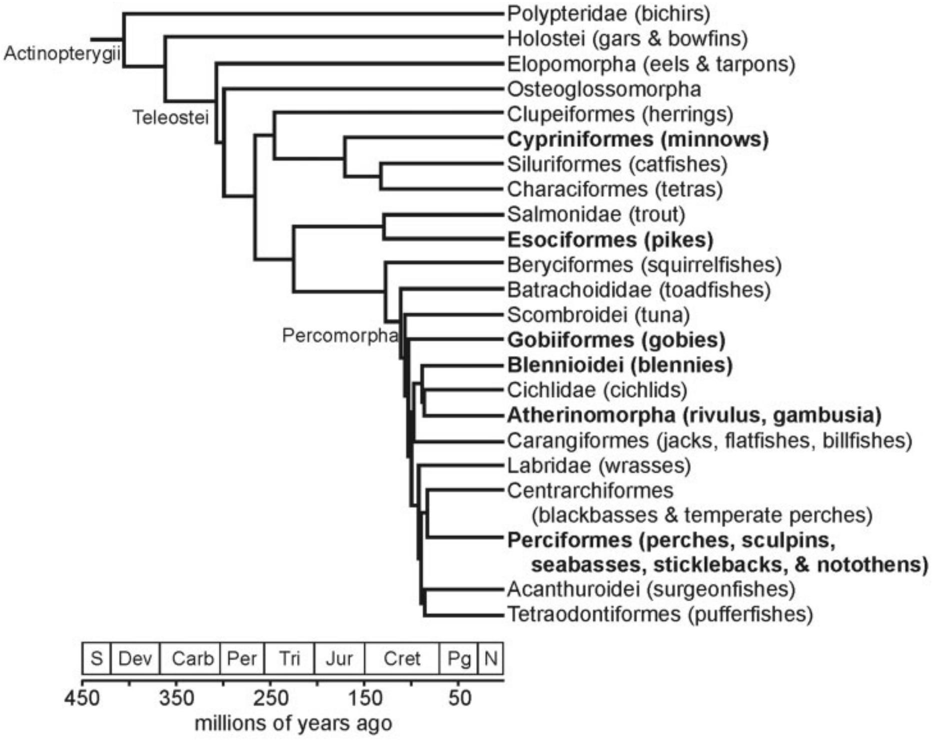

Fig. 1 A time-calibrated molecular phylogeny of the ray-finned fishes (Actinopterygii), where lineages known to contain fish that perform tail-flip and/or prone jumps on land are shown in bold, demonstrates that the ability to jump when on land is present in at least six ray-finned lineages that last shared a common ancestor over 250 million years ago. The phylogeny illustrated here was generated using data presented in Near et al. (2012); abbreviations in the boxes at the bottom of the figure represent geologic time periods, abbreviated as follows: S, Silurian; Dev, Devonian; Carb, Carboniferous; Per, Permian; Tri, Triassic; Jur, Jurassic; Cret, Cretaceous; Pg, Paleogene; and N, Neogene.

or tumble downslope and (presumably) back into the water (Boumis and Gibb 2012). In summary, thrashing behavior allows effective downslope movement, but cannot move a fish uphill, nor can thrashing produce directed locomotion across a flat surface. However, we note that this species can be considered fully aquatic, and any individual largemouth bass may never encounter the land during the course of its lifetime. Thus, we posit that there is minimal selection for terrestrial locomotor performance for this species, or for any other teleost species with a similar natural history.

Occasional emersion: tail-flip jumping

In contrast with fully aquatic species such as largemouth bass, which are unlikely to encounter the shore, some teleost species living at the water's edge can, and do, voluntarily emerge from water and repeatedly encounter the dramatically different physical demands of life on land. The best-studied examples of this type of behavior are found within the teleost order Cyprinodontiformes, the killifishes. Within the order, some species, such as *Gambusia affinis* (the mosquitofish), voluntarily strand themselves to escape predators (Bayliss 1982), while others leap across land to move from one habitat to another (Mast 1915), and still others, such as *Kryptolebias marmoratus*, the mangrove rivulus, have adopted a quasi-amphibious habit, wherein individuals in some populations forage above the tideline but others do not (Huehner et al. 1985; Davis et al. 1990). We have found that many cyprinodontiform fishes—and a surprising variety of fishes from diverse teleost orders (Fig. 1), including members of the ‘‘basal’’ teleost lineage Cypriniformes (e.g., zebrafish, *Danio rerio*)—respond to stranding by producing a type of ballistic jump termed a tail-flip (Mast 1915; Gibb et al. 2011). During a tail-flip, the fish, lying on its side, curls the anterior body up and over the tail, and then extends the body to launch off the caudal peduncle into the aerial, or flight phase, of the behavior (Fig. 2B).

Tail-flip jump behaviors are distinct from thrashes in three key ways (Table 1). (1) Thrashes are produced via a series of variable and repeated whole-body axial movements that appear to the casual observer as uncoordinated. In contrast (Fig. 2), the tail-flip jump is a stereotyped, two-stage behavior, in which a defined suite of movements serves to accelerate the body and propel it away from its original position. First, the anterior body peels away from the substrate and

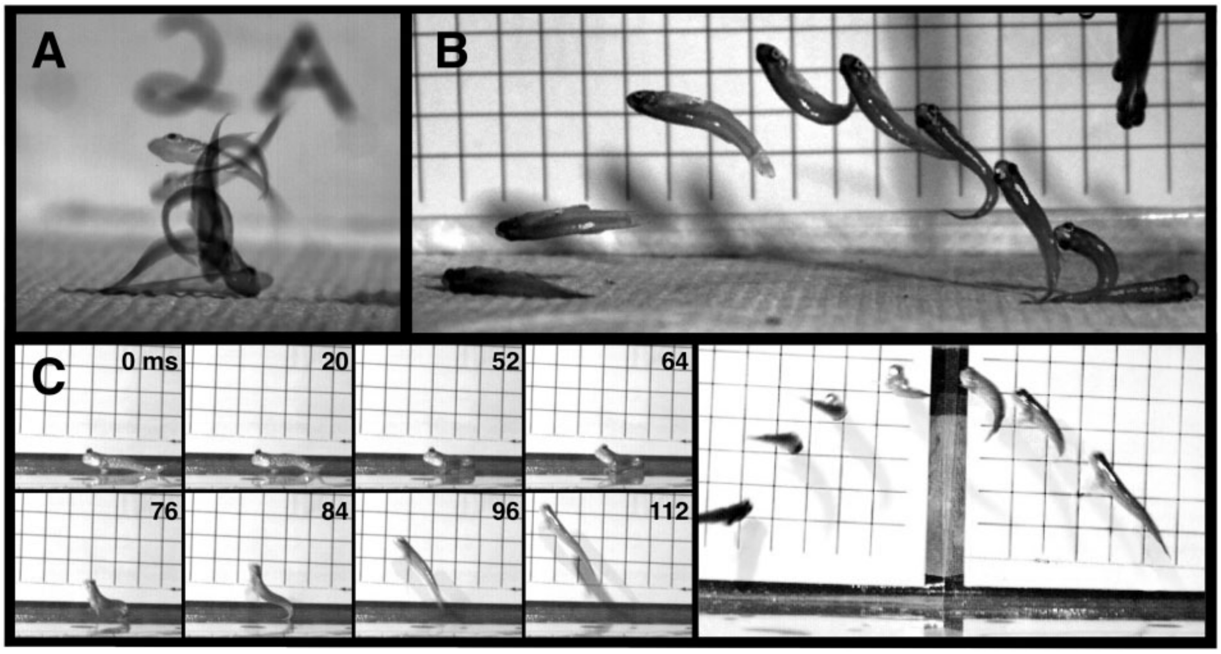

Fig. 2 Thrashes cannot propel juvenile largemouth bass (*Micropterus,* **A**) over a flat surface, whereas tail-flip jumps produce a caudally-directed flight path in the mosquitofish (*Gambusia*, **B**), and prone jumps produce a cranially-directed flight path in the mudskipper (*Periopthalmus,* **C**). Panels are constructed by overlaying consecutive high-speed video images to demonstrate movement over time in a fixed plane of reference, except for stage 1 (axial flexion) and early stage 2 (axial extension) for the mudskipper (**C**), where individual frames (progressing in rows, with time in milliseconds provided within each frame) are given because there is substantial overlap in position of the fish's body from frame-to-frame in successive images. Time increment of frames used to construct the overlay panels are as follows: for *Micropterus* (**A**), 0, 12, 22, 32, 42, 52, and 72 ms; for *Gambusia* (**B**), 0, 58, 76, 98, 122, 148, 183, 226, and 282 ms for *Periopthalmus* (**C**), 112, 144, 168, 204, 232, 252, and 284 ms. Overlay images were constructed in Pixelmator 1.67 (Pixelmator Team Ltd., London, UK) or Adobe Photoshop (CS3), using layer masks that lightened the background and shadows, but did not otherwise alter the images.

curls over the caudal peduncle, presumably via the contraction of the axial muscle along the body on the concave side of the bend (stage 1). Second, the body axis straightens, presumably by recruiting the contralateral musculature (stage 2). We note that this movement pattern is superficially similar to the fast-start behavior that is ubiquitous among teleosts (Domenici and Blake 1997), but that the timing of the behavior—which is consistently much slower on land than in water (Gibb et al. 2011)—makes it unlikely that the same motor pattern underlies both behaviors. (2) On a flat surface (0°) grade, thrashes can propel a fish off the substrate, but thrashes tend to produce ineffective and highly variable take-off angles that generate little overland displacement (Fig. 3). In contrast, tail-flipping species consistently take-off from the ground at angles of 40–80°, which can propel a fish more than five body lengths as a result of a single tail-flip (defined here as stage 1 + stage 2 + aerial phase). (3) Finally, because both the number and timing of axial movements are variable in thrashing species, the location of the body at the end of a thrashing event is unpredictable; in contrast, a tail-flip always generates a predictable escape trajectory as the body is "vaulted" over the caudal peduncle and fin, which remain in contact with the ground until the end of stage 2 (Fig. 2). Thus, the coordinated, stereotyped, two-stage sequence of the tail-flip jump produces a directed, effective movement over a flat surface for all of the species that possess this ability.

Frequent emersion: prone jumping

At the far end of the aquatic-to-terrestrial continuum are terrestrial specialists, such as mudskippers (*Periopthalmus*) and amphibious blennies (*Alticus*) that may spend more than 50% of their lives out of water (Martin and Lighton 1989; Brown et al. 1991; Graham 1997; Gordon 1998; Bhikajee et al. 2006; Hsieh 2010; Ord and Hsieh 2011). Although mudskippers and blennies are not closely related (Near et al. 2012; Fig. 1), in both instances individuals are able to produce directed, coordinated jumps from a prone (i.e., lying on their ventral aspect) position (hence, "prone jumps"). Prone jumps are executed when fish bend the body to bring the tail cranially, place the tail against the substrate in close proximity to the head, and push off with the tail while straightening the body to leap away from the starting position (Fig. 2C). Prone jumps are superficially similar to tail-flip jumps (and aquatic fast starts) in that both behaviors are powered by an initial whole-body bend to one side, followed by extension of the body. For both tail-flip jumps and prone jumps, body extension transmits propulsive forces to the substrate through the caudal peduncle and fin, catapulting the fish into the ballistic, aerial phase.

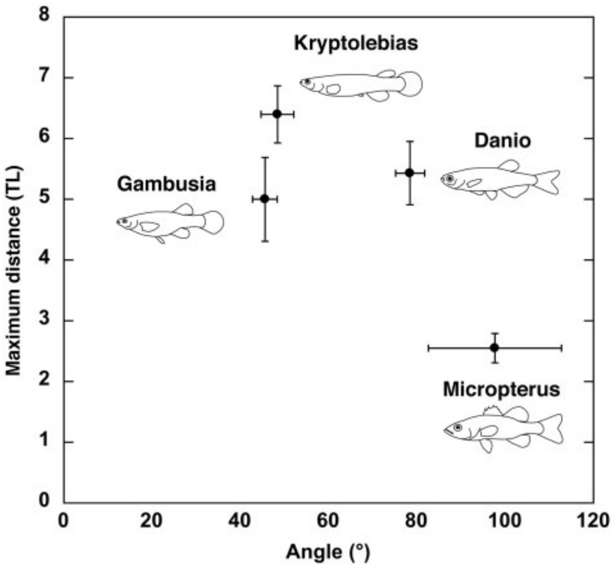

Fig. 3 Angle of take-off (°) and distance traveled (in body lengths) during stranding trials, as measured in four littoral teleost species that represent a variety of natural-history strategies (see text for details), reveals that variation in behavior is associated with variation in locomotor performance. Angle of take-off indicates the angle of the body relative to the substrate when the fish leaves the ground. The tail-flip jumpers, mangrove rivulus (*Kryptolebias*, $n = 30$), mosquitofish (*Gambusia*, $n = 12$), and zebrafish (*Danio*, $n = 10$), can all produce effective overland movements by leaving the ground at <90°. In contrast, thrashing in the largemouth bass (*Micropterus*, $n = 20$) generates highly variable behavior that results in relatively little distance traveled across a flat surface. Individuals were size-matched across all four species, such that mean total length was 3.4 cm (range in mean size for a given species = 3.1–3.6 cm); bars indicate one standard error of the mean.

Prone jumps, however, are distinct from tail-flip jumps in a number of ways (Table 1). (1) Tail-flip jumps are performed from a starting position in which the lateral body surface is in contact with the substrate, and are characterized by the body bending upwards, out of the plane of the substrate—thus the head is cantilevered over the tail. Prone jumps, in contrast, are performed from a starting position in which the ventral surface of the body is in contact with the ground, and are characterized by the body bending in a plane parallel to the substrate to swing the tail anteriorly (Figs. 2C and 5). (2) During a tail-flip jump, the COM moves upward

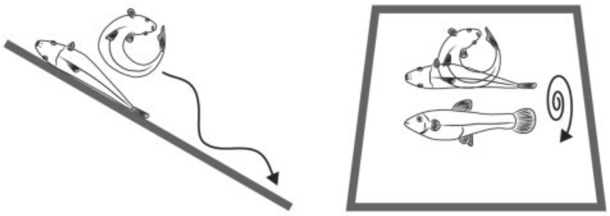

Fig. 4 When fish are stranded on a slope, thrashing—produced by either a single axial bend or a series of side-to-side axial bends—destabilizes the center of mass, causing the fish to roll downhill. Line drawings summarize the typical behavioral responses for two littoral teleost species, mosquitofish (*Gambusia*, depicted here) and largemouth bass (*Micropterus*), when individuals are manually placed on a slope (a shallow box placed at a 30° and covered with dampened sand) with the long-axis of the body positioned either parallel (left panel) or perpendicular to the grade (right panel).

Table 1 Thrashes, tail-flip jumps and prone jumps are characterized by distinct kinematic patterns and different terrestrial locomotion performance outcomes

	Thrash	Tail-flip jump	Prone jump
Phases	Variable	Stereotyped: bending + extension + aerial	Stereotyped: bending + pause + extension + aerial
Body orientation in repose	Lateral body aspect in contact with substrate	Lateral body aspect in contact with substrate[a]	Ventral body aspect in contact with substrate
Plane of body bending	Perpendicular to substrate	Perpendicular to substrate	Parallel to substrate
Directionality of bending	Head and tail toward one another	Head toward tail	Tail toward head
Take-off orientation	Variable	Caudal	Cranial
Take-off angle	∼100°, highly variable	∼40–80°	∼25–60° (*Periopthalmus*); ∼60° (*Alticus*)
Maximum distance	<3 BL	∼5–7 BL	Unknown

[a] With the exception of the mangrove rivulus, *Kryptolebias marmoratus*, see text for details.

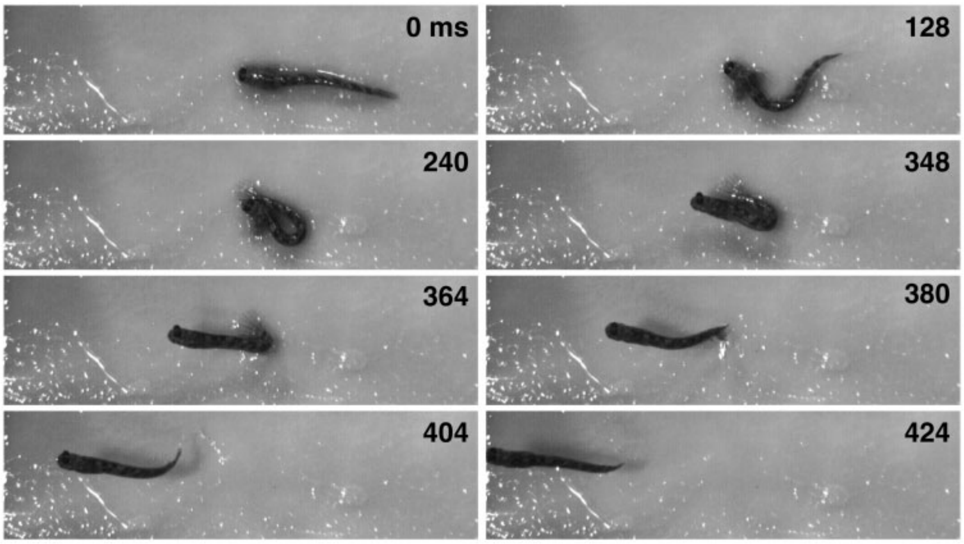

Fig. 5 During prone-jumps in the Pacific leaping blenny, *Alticus*, the body is held in repose with the ventral body surface in contact with the substrate, the tail is then brought anteriorly, and placed on the substrate. Rapid extension of the body generates a controlled and cranially-directed flight trajectory. Panels are comprised of individual frames (with time given in ms) taken from a single jump. Pacific leaping blennies and other blennies that spend extended periods of time on land exhibit a behavioral innovation wherein the tail twists about the long axis of the body, thus maximizing contact between the lateral surface of the tail and the substrate (240–364 ms). Panels are constructed using consecutive frames from high-speed video footage of the behavior.

and over the tail during the initial body bend (stage 1) and continues to move as the axial body is extended (stage 2); whereas during a prone jump, the COM remains static during stage 1, and only moves during stage 2 (Swanson and Gibb 2004; Hsieh 2010). Interestingly, prone jumps both in mudskippers and amphibious blennies are characterized by a "pause" phase, wherein the body does not move for an interval of time (~55–60 ms in the terrestrial specialist blennies *Alticus* and *Andamia*) (Hsieh 2010) in between stage 1 and stage 2. We suggest that pre-activation of lateral myomeres (the axial body musculature) on the convex side of the axial body and tail may occur during this pause to enhance propulsive power during the subsequent launch phase (stage 2). (3) During a tail-flip jump, because the head is initially bent up and over the body, the take-off trajectory propels the fish into a caudally-directed flight path. For prone jumpers, because the tail pushes against the substrate when positioned beside the head, the result is a cranially-directed flight path (Fig. 5).

The prone jump provides two apparent advantages over the tail-flip jump. First, because prone-jumping fishes are positioned on their ventral surfaces at the beginning of the jump, they can readily monitor the world around them with their cephalic sensory systems (especially vision), whereas tail-flip jumpers typically lie on their lateral surface with one eye coming into direct contact with a potentially abrasive substrate. Second, the cranially-directed flight trajectory of prone jumpers allows them to see where they are going prior to jumping and, potentially, to anticipate landing in a specific location; tail-flip jumpers are forced, by the nature of the caudally-oriented jump, to propel themselves into what is likely to be terra incognita.

Tail twisting: a kinematic innovation that enhances jumping performance?

Although a prone posture likely provides the benefit of elevating both eyes to continuously survey the surroundings, it poses a potential problem for terrestrial jumping because the upright caudal peduncle and fin are no longer in an effective orientation for maximally directing propulsive forces against the ground. For example, blenny species that only periodically emerge from water appear to lack control during take-off, as the ventral tail surface sweeps laterally along the ground: note the yawing during the flight phase in Fig. 1C of Hsieh (2010). However, two blenny species, *Alticus* and *Andamia*, have evolved extreme terrestrial habits; *Alticus*, in particular, seldom enter the water, feed and reproduce on land, and defend terrestrial territories (Bhikajee and Green 2002; Hsieh 2010; Ord and Hsieh 2011). In conjunction with committed terrestrial habits and in absence of any obvious morphological specialization of the axial skeleton, these blenny species have evolved axial "tail-twisting" as a kinematic

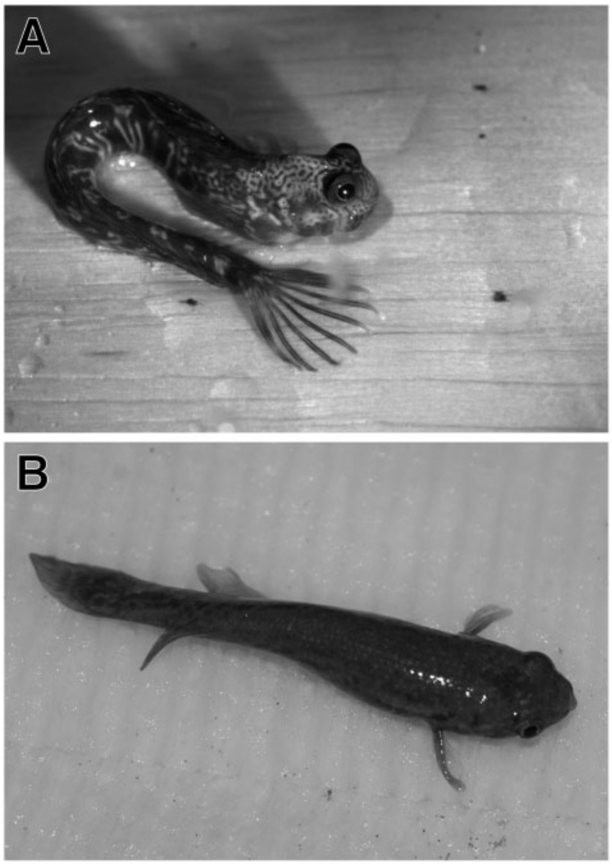

Fig. 6 Both the Pacific leaping blenny (*Alticus*, **A**) and the mangrove rivulus (*Kryptolebias*, **B**) rest on their ventral surface when in repose and rotate the vertebral column about the long axis of the body to place the lateral surface of the tail in contact with the substrate. This convergence in jumping behavior in unrelated taxa suggests that a tail position maximizing contact area of the broader lateral surface is associated with increased terrestriality and enhanced locomotor ability on land.

innovation to facilitate effective locomotion on land (Hsieh 2010). When performing a prone jump, ''terrestrial'' blennies curl the tail toward the head and twist it 90° about the long axis of the body—by rotating the dorsum of the tail and caudal fin out of the mid-sagittal plane and down toward the substrate—thus positioning the contralateral surface of the peduncle against the ground (Fig. 6A). By using the lateral surface of the peduncle, the most terrestrial blennies are able to direct more propulsive force into the ground while also providing a broader base of support, thus preventing slippage of the caudal fin and enabling greater control when jumping, relative to more amphibious sister genera lacking tail-twisting abilities (Hsieh 2010).

How do new behaviors evolve?

Teleost fishes offer an unusual model system in which to examine the evolution of novel behaviors, in part, because the behaviors described here (i.e., thrashes, tail-flips, and prone jumps) appear to represent a true continuum, in which intermediate forms and behaviors are present. In addition, while we have only begun to look for terrestrial behaviors in small littoral fishes, we have already observed terrestrial jumping in six distinct lineages of teleost (Fig. 1): Cypriniformes, Esociformes, Gobiiformes, Blennioidei, Atherinomorpha (including Cyprinodontiformes and Beloniformes), and Perciformes; these lineages last shared a common ancestor during the Permian Era, more than 250 million years ago (Near et al. 2012). Even though it appears we have only encountered the ''tip of the iceberg'' of terrestrial behaviors in teleosts, we have already observed (1) variability in terrestrial behaviors among and within species that likely has functional consequences (Gibb et al. 2011), (2) convergence in key behavioral adaptations for increased terrestriality, and (3) retention of what appear to be ''basal'' behaviors in amphibious fishes that are highly specialized for terrestrial locomotion. Thus, the fact that teleost locomotion on land resembles axial movements used by almost all teleost taxa to produce burst-movements underwater (the aquatic fast start), yet demonstrates diversification in kinematics and performance in the teleost species that spend the most time on land, provides a unique opportunity to address an important evolutionary question: how do new behaviors evolve?

A clear example of a teleost that appears to be evolving a more terrestrial habit is the mangrove rivulus (*K. marmoratus*). Individuals of mangrove rivulus are known to congregate in large numbers inside hollow, rotting logs (Taylor et al. 2008), and feed on terrestrial insects (Huehner et al. 1985; Davis et al. 1990); in addition, individuals of this species can spend up to 66 consecutive days out of water (Taylor 1990). Although mangrove rivulus use tail-flip jumps as their burst terrestrial locomotor behavior, when they repose on land, they readily adopt a prone body position, resting on their ventral aspect. Thus, although mangrove rivulus cannot perform a ''prone jump,'' they evidently have converged on the prone resting posture exhibited by the most terrestrial of fishes—the amphibious blennies and mudskippers. In addition, mangrove rivulus exhibit another behavioral modification that maximizes their locomotor abilities on land; while in the prone posture, they maintain contact of the caudal fin with the ground by twisting the caudal peduncle axially nearly 90° to place the tailfin in contact with the substrate (i.e., they demonstrate tail twisting similar to that of the most terrestrial blennies; Fig. 6).

This may provide an advantage to mangrove rivulus because the caudal peduncle is already in contact with the substrate, thereby minimizing the body-reorientation necessary when quickly rolling onto their lateral surface to produce a tail-flip jump (Supplementary Video S1). Use of tail twisting as a means of increasing jump performance represents another example of convergent evolution of terrestrial locomotor strategy among distant taxa, that is, between the mangrove rivulus, *K. marmoratus*, and the distantly related terrestrial-specialist blennies, *Alticus* and *Andamia*. Thus, the mangrove rivulus provides an excellent example of a true ''intermediate'' form that improves our understanding of how a quasi-amphibious tail-flip jumper might evolve and eventually become a terrestrial specialist that moves about via prone jumps.

Further support for the hypothesis that tail-flip jumps serve as a behavior that facilitates the colonization of the terrestrial realm is demonstrated by the retention of tail-flip jumps by terrestrial specialists. When threatened, mudskippers, and terrestrial blennies typically produce prone jumps (Swanson and Gibb 2004; Hsieh 2010). However, if the negative stimulus is presented near the head, then execution of a prone jump would move the animal toward the stimulus, rather than away. In such situations, mudskippers, and terrestrial blennies both produce tail-flip jumps, in which they curl the head over the tail to propel the fish caudally, away from the potential threat (see Supplementary Video S2). Furthermore, the more aquatic sister genera to the terrestrial blennies show a preference for using tail-flip jumps, independent of stimulus direction. Thus, it seems likely that the ''basal'' tail-flip behavior is retained by terrestrial specialists because it remains useful under specific circumstances.

Functional trade-offs in form and performance

When considering the variation in the ability to move on land among teleosts exhibiting different affinities for the terrestrial environment, the question arises: why don't all teleosts have the ability to move effectively on land? Although there are no studies of which we are aware that examine this question directly, we suggest that two parameters may influence and/or constrain terrestrial locomotor performance: body size and aquatic locomotor performance.

Body size appears to limit the ability of fish to move effectively on land via jumping; to our knowledge, the largest terrestrial jumper is the appropriately named giant mudskipper, *Periophthalmodon schlosseri*, which can reach 30 cm in body length (Mazlan and Rohaya 2008). Larger-bodied teleosts that move on land typically use lateral undulation, (e.g., eels [Anguilidae; Gillis 1998], ropefishes [Polypteridae; Pace and Gibb 2011], and pricklebacks [Stichaeidae; Clardy 2012]), or a complex combination of paired fin and axial body movements, for example, climbing gobies (Gobiidae) (Blob et al. 2006) and walking catfishes (Clariidae) (Pace et al. 2010), instead of tail-flip jumps or prone jumps. There may be an upper size-limit to terrestrial jumping because body mass scales with volume (increasing with length to the cubed power), whereas production of muscular force increases with muscle physiological cross-sectional area (increasing with length to the squared power) (Hill 1950); as a consequence, body mass increases faster than the fishes' ability to produce force. The combination of a relatively conserved body shape (but see below) in combination with the intrinsic mismatch of body-mass-to-force-production likely makes it impossible for fish above a certain body size to produce effective, directed terrestrial jumps.

The potential trade-off between terrestrial and aquatic locomotor performance is another factor that may reduce the ability of some teleosts to move effectively on land. Indeed, even within the aquatic environment, trade-offs between sustained-swimming performance and burst-swimming performance are well-documented; fishes with high steady swimming performance have streamlined shapes and high-aspect-ratio tails, whereas those with high burst performance have deeper bodies and low-aspect-ratio tails (for a review, see Langerhans and Reznick 2009). As a result, we hypothesize that body forms that are most effective at producing terrestrial movements incur a concomitant decrease in performance during key aquatic behaviors. In fact, relative to fully-aquatic species, jumping species tend to be more elongate, have a more constant body depth, and are less laterally compressed—all characteristics that are inconsistent with fusiform, drag-minimizing shapes (McHenry and Lauder 2006). Variation in body shape in teleost fishes can be quantified using the fineness ratio, or body length divided by body depth, where a fusiform, streamlined fish with a drag-minimizing body form has a fineness ratio of 4.5 (Webb 1975). Fishes that spend more and more time out of the water are increasingly subject to the selection pressures of the terrestrial environment, which may drive them away from body shapes that maximize aquatic locomotor performance. This change in body form is perhaps best demonstrated within the blenny family, in which the most terrestrial species have a fineness ratio of approximately 10, and

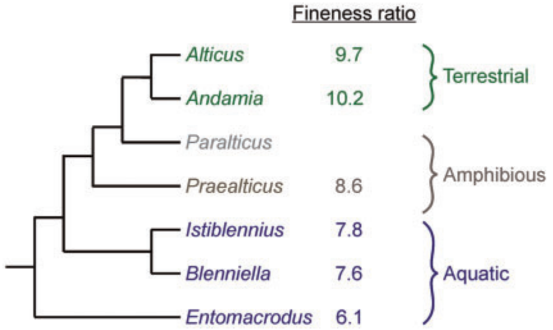

Fig. 7 A phylogeny depicting several genera of intertidal comb-toothed blennies (Salariini) demonstrates that increased fineness ratio (body length divided by body depth) is associated with increased terrestrial specialization (figure modified from that of Hsieh 2010). As intertidal blennies have become increasingly modified for life on land, their body shapes have evolved away from low, drag-minimizing fineness ratios (see text for details).

closely related species that spend most of their lives in the water have fineness ratios of between 6 and 8 (Fig. 7). Thus, evolution of a body shape that facilitates effective terrestrial movement may represent a previously unrecognized axis of variation driving diversification in the teleost body plan.

In addition, musculoskeletal or control-system changes that facilitate movement on land likely come at a cost to aspects of aquatic performance. This is an area of research that has thus far received very little attention; however, we have quantified the time to complete stage 1 of the aquatic fast start in sized-matched individuals from two predominantly-aquatic tail-flip jumpers (zebrafish, *Danio,* and mosquitofish, *Gambusia*) (Gibb et al. 2011), the quasi-amphibious mangrove rivulus (*Kryptolebias*), and the mudskipper (*Periopthalmus*), a terrestrial specialist (Swanson and Gibb 2004). Results of this comparison suggest that, as terrestrial ability increases, the time it takes to complete stage 1 (often considered the preparatory phase) of the fast start increases concomitantly (Fig. 8). Correspondingly, we hypothesize that small juvenile largemouth bass (thrashers) will be able to complete stage 1 more rapidly than do the tail-flip jumpers we have studied to date. Because stage 1 of the fast start in an aquatic habitat results in very little translation of the COM away from a threat, any increased delay before movement should put the fish at a greater risk of being consumed (Walker et al. 2005). Furthermore, this finding suggests that selection for greater performance on land may alter aspects of the musculoskeletal system or neuromechanics at a cost to specific aspects of aquatic fast-start performance.

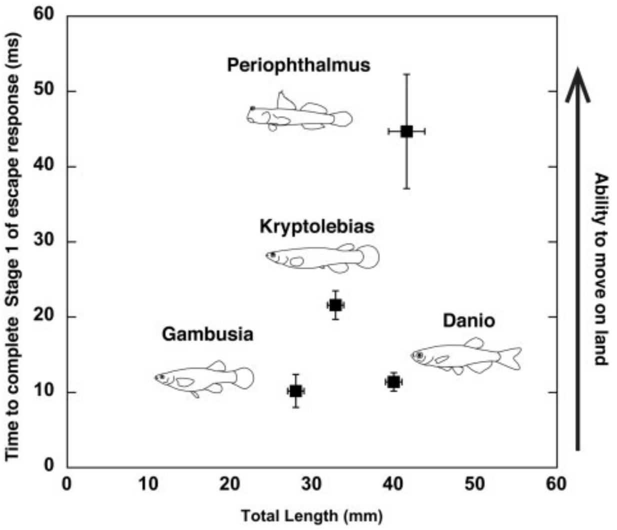

Fig. 8 Variation in the time it takes to complete the preparatory phase (stage 1) of an aquatic fast-start escape response in response to a negative stimulus—as measured for approximately size-matched individuals representing four teleost species with a variety of natural-history strategies—suggests that modifications of the musculoskeletal and control systems for life on land may incur a cost for aquatic locomotor performance. Because stage 1 does not generate significant translation of the center of mass from the starting position, increased delay in completing this stage increases the probability of a fish being consumed by a potential predator. Amphibious mudskippers (*Periopthalmus*) and the quasi-amphibious mangrove rivulus (*Kryptolebias*) exhibit adaptations that enhance jumping performance on land (see text), but take longer to complete stage 1 of the aquatic fast start, relative to similarly-sized zebrafish (*Danio*) and mosquitofish (*Gambusia*); error bars indicate one standard error of the mean.

Summary and conclusions

Although voluntary terrestrial emergence is surprisingly common among teleosts, it is even more remarkable that some ability to move on land may be ubiquitous among what are often considered to be fully-aquatic teleost species. Unlike early tetrapodomorphs, most teleosts do not exhibit modularity, that is, they have not partitioned the axial and appendicular systems in ways that accommodate different aquatic and terrestrial locomotor functions. Rather, most extant teleosts appear to use two distinct neural control patterns that drive the axial musculoskeletal system to produce movement both in water and on land. However, the ability of teleosts to produce directed movement on a flat surface varies dramatically according to their natural history. Fully-aquatic species that have only incidental contact with the terrestrial environment—through accidental stranding, for example—are unable to make directed overland movements. Yet, species that experience only incidental emersion can still employ thrashing, a behavior that is characterized by sequential side-to-side bending, and that de-stabilizes the center of mass to roll downhill and toward the likely location of a standing body of water. In contrast, species that have evolved adaptations permitting occasional emergence from the water typically employ tail-flip jumping, in which a stereotyped, two-stage, flexion plus extension generates a directed and predictable flight trajectory. Tail-flip jumps can be of high performance, resulting in translations exceeding five body lengths at a time. However, a tail-flip jump begins with the fish lying on its side, usually with one eye pressed against a potentially abrasive surface, and does not appear to permit anticipatory or ''goal-driven'' jumps because it is unlikely that the fish can see (or otherwise sense) where it is headed during the flight phase. The most derived terrestrial jumping mode is prone jumping, which is performed by terrestrial specialists that emerge frequently from the water and have become truly amphibious. During a prone jump, the fish rests on its ventral surface, the tail curls toward the head, and the flight path is directed cranially. Presumably, this allows the fish to anticipate where it will land, and possibly to target a specific landing location. In some of these terrestrial specialists, the kinematic innovation of tail twisting appears to enhance the stability and effectiveness of the jump by improving contact between the propulsive appendage and the substrate.

Terrestrial locomotion in teleosts appears to have arisen via a ''repurposing'' of musculoskeletal systems that evolved as mechanisms powering aquatic locomotory bursts. We note that both types of directed jumping behaviors (tail-flips and prone jumps) are powered by the large mass of fast-glycolytic (''white'') fibers that forms the bulk of the myomeres (the lateral musculature) of all teleost fishes, and in both instances this muscle is recruited by the nervous system to generate a ballistic launch. In addition, both tail-flip jumps and prone jumps are characterized by a two-phase movement consisting of flexion followed by extension of the body. Similarly, the aquatic fast-start, another burst behavior, is also driven by recruitment of the axial myomeres and is characterized by a two-phase flexion-then-extension movement. Thus, the convergence in broad kinematic patterns between both types of jumps and the aquatic fast start suggests that jumps are simply an exaptation of a neuromuscular system that powers unsteady behaviors in the aquatic realm. In addition, because elastic storage of energy is critical for increasing the efficiency of locomotion in many organisms in water, on land, and in the air (e.g., Summers and Long 2006), it is likely that during terrestrial jumps and aquatic fast-starts the entire body (i.e., vertebral column, axial musculature, and skin) is loaded with elastic energy during the bending phase, and this stored energy is used to power rapid acceleration during the extension phase. Indeed, the similarities in pattern of movement among all four behaviors (aquatic fast starts, thrashing, tail-flips, and prone jumps) may reflect a kind of biomechanical convergence for more efficient burst movements; during flexion, the body stores energy in compression and then recoils to transmit this energy to the environment.

It is important to note, however, that while there are similarities in overall movement patterns for burst behaviors across these two disparate environments, the ability to locomote under such different physical regimes subjects these fishes to unavoidable biomechanical trade-offs. It is likely that effective locomotor performance on land requires a restructuring of the musculoskeletal system that is in direct conflict with the requirements of a low-drag, fusiform body shape. Such physical constraints may explain why a fish like the largemouth bass is unable to jump on land—the potential sacrifice in aquatic swimming performance is simply too great. In addition, when fishes are underwater, their weight is supported by buoyant forces from the surrounding water; however, upon emergence into the terrestrial realm, gravity places the body under increased mechanical load. This new mechanical load may place an upper size limit on a species' ability to jump on land—which, in turn, could constrain which species are able to make the evolutionary transition to land.

Because they are exceptionally diverse in phylogeny, morphology, and natural history, extant teleosts offer a unique opportunity to explore the evolutionary, physiological, behavioral, and morphological characteristics that enable one organism to span two physically disparate environments in a single lifetime, or even within a given day. Indeed, for teleost fishes that live in close proximity to the land, some degree of locomotor performance in both environments must be maintained—which suggests that selective pressures experienced in both environments may work together to favor morphologies and behaviors that represent biomechanical ''compromises.'' We suggest that a greater appreciation for the range of strategies employed and the evolutionary selective pressures driving the acquisition of new adaptive traits and behaviors in this highly-tractable model system will prove invaluable for gaining an understanding of the challenges that past, present, and future vertebrates living at the water's edge must overcome to successfully navigate the evolutionary transition to life on land.

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Supplementary Data

Supplementary Data available at *ICB* online.

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