RESEARCH ARTICLE

JOURNAL OF
EXPERIMENTAL
ZOOLOGY
PART A
ECOLOGICAL GENETICS AND PHYSIOLOGY
A Journal of Integrative Biology

Fish Out of Water: Terrestrial Jumping by Fully Aquatic Fishes

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ABSTRACT Many teleosts that live at the water's edge will voluntarily strand themselves to evade predators or escape poor conditions—this behavior has been repeatedly observed in the field for killifishes (Cyprinodontiformes). Although most killifishes are considered fully aquatic and possess no obvious morphological specializations to facilitate terrestrial locomotion, individuals from several different species have been observed moving across land via a "tail flip" behavior that generates a terrestrial jump. Like aquatic fast starts, terrestrial jumps are produced by high-curvature lateral flexion of the body (stage one), followed by contralateral flexion of the posterior body (stage two). Here, terrestrial jumps and aquatic fast starts are quantified for two littoral teleosts: *Gambusia affinis* (a killifish, Cyprinodontiformes) and *Danio rerio* (a small carp, Cypriniformes) to determine if the tail flip is produced by other (non-killifish) teleosts and to test the null hypothesis that the tail flip is a fast start behavior, performed on land. Both *Danio* and *Gambusia* produce tail flip-driven terrestrial jumps, which are kinematically distinct from aquatic escapes and characterized by (1) a prolonged stage one, during which the fish bends, lifting and rolling the center of mass over the caudal peduncle, and (2) a relatively brief stage two, wherein the caudal peduncle pushes against the substrate to launch the fish into the aerial phase. The ability of these fully aquatic fishes to employ the same structure to produce distinct kinematic patterns in disparate environments suggests that a new behavior has evolved to facilitate movement on land and that anatomical novelty is not a prerequisite for effective terrestrial locomotion. *J. Exp. Zool. 313A, 2011.* © 2011 Wiley Periodicals, Inc.

J. Exp. Zool. 313A, 2011

How to cite this article: Gibb AC, Ashley-Ross MA, Pace CM, Long JH Jr. 2011. Fish out of water: terrestrial jumping by fully aquatic fishes. J. Exp. Zool. 313A:[page range].

Many teleost fishes that live at the water's edge, such as the killifishes (Cyprinodontiformes), will leap out of the water to evade predators (Bayliss, '82) or escape poor water conditions (Mast, '15), voluntarily stranding themselves on land. Although such non-amphibious fishes must quickly return to the water or risk dying from asphyxiation or desiccation, most killifishes are fully aquatic and have no apparent morphological specializations of the postcranial skeleton to facilitate movement on land (Parenti, '93). However, researchers studying the ecology and behavior of killifishes in the field have repeatedly observed these fishes performing a coordinated locomotor behavior—often described as a "tail flip"—in response to both voluntary and involuntary stranding (Meeks, 1895, '15; Goodyear, '70; Seghers, '78).

In fact, a stranded killifish can employ the tail flip behavior to produce a terrestrial jump with a flight phase that displaces the fish several body lengths away from its original location (Fig. 1A). The movement pattern that characterizes the tail flip appears to be similar to that of the aquatic fast start escape response (Eaton et al., 2001): high-curvature lateral flexion of the body (stage one), followed by contralateral flexion of the posterior body (stage two). The superficial similarity of these two behaviors suggests a hypothesis that could explain how a fully aquatic fish can move effectively

Grant Sponsor: NSF; Grant numbers: IOS-0726001; IOS-0922605.

Additional Supporting Information may be found in the online version of this article.

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Received 20 April 2011; Revised 16 August 2011; Accepted 24 August 2011

DOI: 10.1002/jez.711

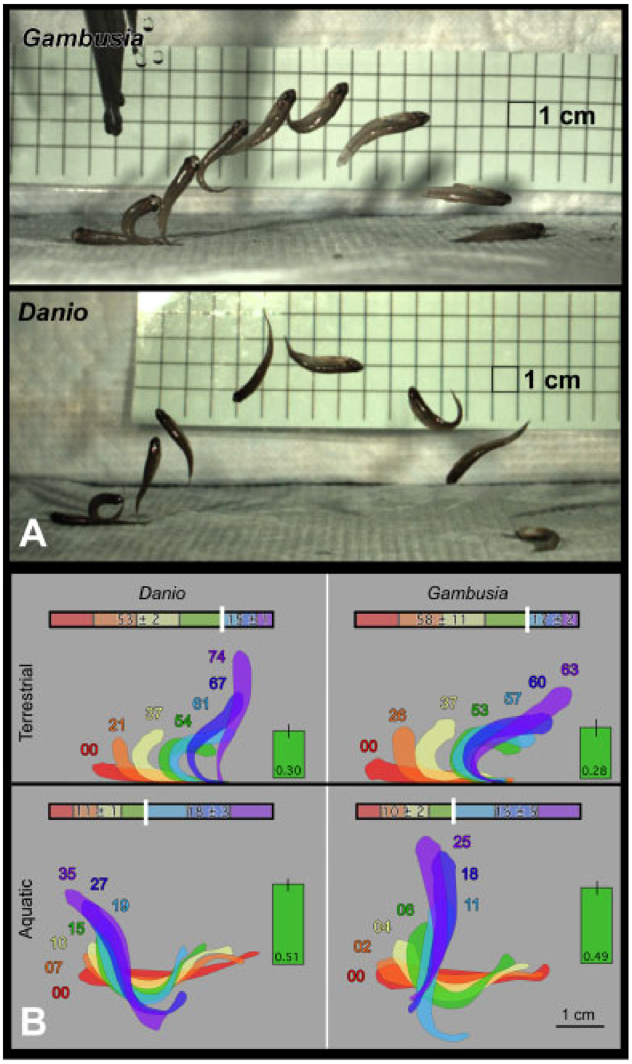

Figure 1. (A) Two small teleosts (*Danio* and *Gambusia*, with metal spatula being withdrawn from arena at left) produce terrestrial jumps that appear superficially similar to the aquatic fast start. Adobe Photoshop was used to crop, flip, adjust brightness/contrast, and layer ("darken" filter) nonconsecutive sequential images, but no other manipulations were performed; unprocessed source video can be viewed as *Electronic Supplementary Material.* (B) Terrestrial jumping is distinct from an aquatic fast start: body outlines (time in *ms*) illustrate representative terrestrial (top panels, lateral view) and aquatic behaviors (bottom panels, dorsal view) for *Danio* (left) and *Gambusia* (right). Within each panel, the multicolored bar indicates the duration (mean ± 1 SE) of stages one and two, the vertical white line delineates the completion of stage one, and the green column represents maximum curvature at the end of stage one (mean ± 1 SE).

on land: an aquatic fast start behavior is generated in response to stranding, and this stereotypical movement pattern produces a jump when executed in the distinct physical regime of the terrestrial environment (Biewener and Gillis, '99; Swanson and Gibb, 2004).

To assess this hypothesis, we compared aquatic fast starts with tail flip-driven terrestrial jumps in two littoral teleosts: a killifish, *Gambusia affinis* (mosquitofish, Cyprinodontiformes), and a small cyprinid, *Danio rerio* (zebrafish, Cypriniformes). *Gambusia* were chosen because they will voluntarily strand themselves to evade predators (Bayliss, '82); *Danio* are not known to emerge onto land voluntarily, are distantly related to *Gambusia* (the last common ancestor lived ~150 mya; Carroll, '88), and are included here to discern if tail flip-driven terrestrial jumping is present in a non-killifish teleost of similar adult body size. Despite the markedly different physical conditions of land vs. water, it is possible for a fish to retain key characteristics of a given behavior across physically disparate environments (Swanson and Gibb, 2004; see also Discussion). Thus, following the null hypothesis that a tail flip is an aquatic fast start performed on land, we predict that key aspects of the movement pattern are similar across environments: (1) absolute duration of stage one, (2) absolute duration of stage two, (3) relative durations of stages one and two, and (4) maximum curvature produced during stage one—as measured by the curvature coefficient, the minimum distance between the head and the tail at the time of maximum bending divided by the fish's body length (Brainerd and Patek, '98).

MATERIAL AND METHODS

Individuals (ten individuals of each species, with five individuals tested in each environment for a total $n = 20$) of *D. rerio* (Hamilton, 1822; http://en.wikipedia.org/wiki/Author_citation_(zoology)) and *G. affinis* (Baird and Girard, 1853) were digitally imaged fast starting in water (aquatic) and jumping on land (terrestrial) at 20 ± 1°C. For terrestrial trials, fish were positioned on a moist, paper covered, flat surface; wet lab bench paper was selected as the terrestrial substrate because it prevented desiccation and provided friction to enhance ground contact, but did not degrade the fish's slime coat. The response to stranding was recorded at 700 fps from a lateral aspect (Fig. 1A and B), using a Vision Research Phantom V5 (Vision Research, Inc. Wayne, NJ 07470) digital-imaging system. Body landmarks (tip of snout, tip of tail, pectoral girdle) were tracked using ImageJ (Research Services Branch National Institute of Mental Health, Bethesda, MD 20892; Rasband, 2008) to ascertain bending pattern (head toward tail, tail and head toward one another, or tail toward head), curvature coefficient (Brainerd and Patek, '98), durations of stages one and two (ms), and take-off angle (vertex of the mid-sagittal plane of the anterior body with a line parallel to the horizon). For aquatic trials, fish were placed in a water filled (~6 cm depth) glass bowl, and escape behaviors were elicited using a negative visual or mechanical stimulus. Aquatic fast starts were recorded (700 or 1,000 fps) from the dorsal aspect (Fig. 1B) and variables measured as described above. Multiple events (2–5) *per* individual were recorded and the event with the optimal body orientation (on land, long axis of the body perpendicular to camera lens to minimize image parallax; in water, fish in middle of arena to minimize wall effects) was selected for kinematic analysis.

Two-way ANOVAs (PSAWStatistics18, SPSS) evaluated potential effects of "species" and "environment"; as there were no significant species-by-environment interactions (all $P > 0.5$), the term was removed from the models (Sokal and Rohlf, '95). A significant effect of environment would support the hypothesis that movements produced on land are distinct from those produced in water. An additional one-way ANOVA was conducted on the variable "take-off angle" to evaluate potential differences in jumping between species. All procedures were conducted in accordance with Northern Arizona University's IACUC Protocol #09-009.

RESULTS

For all two-way ANOVAs, there was a significant effect of environment (all d.f. = 1,17; $F > 24$; $P < 0.001$), but no effect of species (all d.f. = 1,17; $F < 0.3$; $P > 0.05$). During the fast start, the head and tail bend toward one another, about the center of mass (COM; near the pectoral girdle); however, during the terrestrial jump, a fish "peels" the anterior body from the substrate and rolls toward the tail, using momentum augmented by the push of the caudal peduncle against the ground to launch into ballistic flight (Fig. 1A). Jumping is characterized by greater stage one curvature (a smaller curvature coefficient), relative to the fast start (Fig. 1B; Table 1). Terrestrial jumps are slower than fast starts, and stage one always comprises a greater proportion of the total event (Fig. 1B; Table 1). At the end of stage two, *Danio* and *Gambusia* enter the flight phase of the jump at different take-off angles (one-way ANOVA d.f. = 1,8; $F = 14$; $P < 0.01$; Table 1).

DISCUSSION

The disparate physical forces of the aquatic vs. terrestrial environment do not necessarily impose physical constraints on a behavior that will obscure key kinematic characteristics. Even when completely submerged, amphibious mudskippers (*Periophthalmus argentilineatus*, Perciformes, Oxudercinae) will occasionally produce an aquatic behavior that is indistinguishable from a terrestrial "jump" (Swanson and Gibb, 2004). In contrast with this finding for mudskippers and contrary to our original predictions, terrestrial jumps and aquatic fasts starts in the two fully aquatic teleost fishes examined here are characterized by distinct kinematic patterns, which suggest that the axial musculature is recruited differently across environments to produce two distinct behaviors.

For *Gambusia* and *Danio*, the differences in behavior across environment are particularly extreme during stage one, which takes five times longer during the terrestrial jump than during the aquatic fast start. This change in timing suggests a corresponding change in muscle activation when the fish is on land: either the duration of muscle activation and contraction during stage one is longer or there is a delay between activation offset at the end of stage one and activation onset at the beginning of stage two. During stage one of the terrestrial jump, the COM is lifted off the ground and accelerated toward the tail. Although it is possible that a combination of passive stiffness and inertia are sufficient to maintain momentum, we posit that the contralateral musculature is activated throughout stage one to support the body against the countervailing force of gravity. Contralateral axial muscle activity—not typically present in a fast start (Jayne and Lauder, '93)—may also be required to stabilize the posterior body and caudal peduncle during stage one and the anterior body during stage two. However, studies quantifying muscle activity in both environments are necessary to verify that a distinct motor pattern produces the terrestrial jump.

One likely function of the prolonged stage one that characterizes the terrestrial jump is to load body tissues with elastic energy. When the COM moves over the caudal peduncle during stage one, the posterior body is bent maximally. Because bent fish bodies can store elastic energy (Summers and Long, 2006), elastic recoil may help power COM acceleration during stage two—enabling the fish to "spring" into the air. Interestingly, although vertically oriented axial bending is characteristic of tail flip-driven jumping, it is *not* present in all fishes that jump on land. Many fishes that repeatedly emerge as part of their life history, including the mudskippers mentioned above (Swanson and Gibb, 2004), "terrestrial" blennies [Perciformes, Blenniidae (Hsieh, 2010)] and tidepool gobies [Perciformes, Gobiidae (Aronson, '71)] jump using laterally oriented axial bending—wherein the fish rests on its ventral (rather than

Table 1. Kinematic variables (mean ± SE) characterizing aquatic fast starts and tail flip-driven terrestrial jumps in *Danio rerio* and *Gambusia affinis*

Environment	Species	Length (mm)	Stage 1 duration (ms)	Stage 2 duration (ms)	Stage 1/ Stage 2	Curvature coefficient	Take-off angle (°)
Aquatic	*Danio*	40±1	11.4±1.2	17.5±2.8	0.70±0.04	0.51±0.02	*N.A.*
Aquatic	*Gambusia*	28±1	10.2±2.2	15.4±5.1	0.75±0.04	0.49±0.02	*N.A.*
Terrestrial	*Danio*	31±2	53.1±2.2	15.1±1.1	3.5±0.18	0.30±0.02	45.5±2.8
Terrestrial	*Gambusia*	30±4	58.0±10.7	17.3±2.0	3.3±0.13	0.29±0.03	78.4±3.3

lateral) surface, bends the tail toward the head (rather than bending the head toward the tail), and presses the caudal peduncle onto the substrate to launch into the flight phase. Because these amphibious fishes bend their bodies in a plane parallel to the ground, stage one movements cannot harness gravitational forces to facilitate storage and recovery of elastic energy.

Although *Danio* and *Gambusia* both produce a tail flip-driven terrestrial jump, this behavior does seem to vary between the two species. *Gambusia* is, at least in one sense, a "better" jumper because they take off at ~46° mean launch angle, which should enable them to travel farther per unit effort, relative to *Danio*, which take off at ~78° mean launch angle. In addition, during the stage one phase of some tail flips, the posterior body will bend upward and lose contact with the ground; although loss of contact can occur in either species, it is more common in *Danio* (Fig. 1A). We also note that *Danio* tend to flip end-over-end during the flight phase, whereas *Gambusia* are more likely to maintain their head and upper body in a stable attitude (Fig. 1A), with the head remaining oriented in the direction of travel throughout the flight phase.

The lack of apparent morphological specialization for terrestrial locomotion and the vast phylogenetic distance between these two taxa generates an unexpected question: is the ability to jump on land when stranded a shared trait of the Telostei that has been lost in some lineages? It seems likely that changes to body proportions and/or axial stiffness could reduce jumping ability in taxa with specialized, nonfusiform body shapes. In addition, because the force generated by muscles increases in proportion with the muscles' cross-sectional area while the body mass displaced increases in proportion with the body's volume (Hill, '50), physical constraints imposed by scaling may make terrestrial jumping impossible for large individuals. Ongoing work in our laboratories will determine which teleost lineages possess the ability to jump on land, ascertain at what body size terrestrial jumping becomes impractical (or impossible), and establish which (if any) aspects of body allometry constrain terrestrial jumping performance.

We conclude with the observation that, although several studies have examined the postcranial anatomy of the species considered here (e.g., Bird and Mabee, 2003; Parenti, '93), no one has ever suggested that individuals of *G. affinis* or *D. rerio* are anatomically specialized for life on land—nor is there any a priori reason to posit that anatomical modifications are required to produce a tail flip-driven terrestrial jump. We find that two teleost species that differ in their propensity to emerge from water both employ the same structure (axial musculature plus caudal peduncle) to produce superficially similar but kinematically distinct behaviors across disparate physical environments. This finding supports the "behavioral drive" paradigm of evolution (Mayr, '63): new behaviors can arise in the absence of obvious morphological specialization and anatomical novelty does not seem to be a prerequisite for the physical demands of the terrestrial environment.

ACKNOWLEDGMENTS

Financial support was provided by NSF IOS-0726001 to ACG and NSF IOS-0922605 to JHL. Northern Arizona University undergraduates Michael Ackland, Jenny Eckle, and Audriana Hurbon assisted with data collection. Helpful feedback on the manuscript was provided by Drs. Lara Ferry and Marianne Porter and two anonymous reviewers.

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