Jumping in the Salamander *Desmognathus ocoee*

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Unlike most terrestrial vertebrates, which use force generated from the hind limbs to jump, salamanders jump by laterally bending and then rapidly straightening the body, using momentum to carry the individual through the air. This movement is strikingly similar to both the terrestrial escape response of mudskippers and terrestrial blennies, and shares a general pattern of movement with the C-start escape response in several aquatic vertebrates. While the axial musculature appears to be responsible for this behavior, it remains to be seen what role the limbs and tail play. Across a two-fold range in body sizes, few kinematic parameters were correlated with size. The lack of strong scaling relationships suggests a spring mechanism that allows performance to be maintained despite a two-fold increase in size.

PLETHODONTID salamanders, a diverse group of lungless amphibians, possess a myriad of defensive mechanisms to deter predation (Brodie, 1977; Brandon et al., 1979). Individual species exhibit passive mechanisms, including aposematic coloration and toxins secreted through skin (Brandon et al., 1979). These salamanders also incorporate a range of active mechanisms to avoid predation, including coiling, lashing, writhing, or in some cases remaining completely motionless (Brodie, 1977). One species, *Hydromantes platycephalus*, has been documented rolling itself downhill to escape (Garcia-Paris and Deban, 1995).

One mechanism of escape in aquatic salamanders is the C-start or fast-start escape response. Well studied in fish, the C-start escape is a two stage response: Stage 1 is defined by axial bending with little effect on the individual's center of mass; Stage 2 being the rapid straightening of the body, the resulting wave propelling the individual away from the stimulus (Weihs, 1973). In fish, this escape response is controlled by Mauthner neurons (Eaton et al., 1977), and has been suggested as a possible control mechanism for the escape response in some aquatic salamanders (Azizi and Landberg, 2002). In *Eurycea bislineata*, both adults and larvae use the C-start in response to a tactile stimulus in an aquatic environment (Azizi and Landberg, 2002). However, it remains unclear whether the Mauthner neurons are present in many species of salamander (Nishikawa et al., 1991; Will, 1991) or if they play a role in the generation of this behavior (Azizi and Landberg, 2002).

This study details a previously undescribed mechanism of terrestrial jumping in the plethodontid salamander, *Desmognathus ocoee*. This mechanism of movement has been mentioned anecdotally as a defensive behavior (Cochran, 1911; Murphy, 1917; Brodie, 1977; O'Reilly et al., 2000), but the mechanics of the movement have yet to be described. In this study, high speed imaging was used to describe the mechanism by which the salamanders are able to propel themselves through the air. It is hypothesized that the hind limbs are responsible for providing a pushing-off point, but that the axial muscles are the primary force in jumping, as plethodontid salamanders lack the large limbs common in other taxa whose jumping performance has been measured (e.g., fleas [Bennet-Clark and Lucey, 1967], frogs [Marsh, 1994], kangaroos [Alexander and Vernon, 1975]).

The second aim of this study is to quantify the effects of body size on this jumping behavior. The scaling of morphology and behavior has long been of interest to biologists, particularly the impacts of scaling on physiological processes (Hill, 1950; Schmidt-Nielsen, 1984). Within amphibians, most work has focused on the scaling of feeding systems and the implications of changing size on the ability to acquire and process food (Reilly, 1995; Deban and O'Reilly, 2005; Ryerson and Deban, 2010). For jumping, I expect the kinematic variables measured will match those predicted by geometric similarity (Hill, 1950). For Hill's (1950) model, predictions are based on muscle physiology; for animals that are geometrically similar, absolute jump distance should be the same. Larger animals will have slower linear accelerations, resulting from larger muscles that must contract greater linear distances. Smaller animals, despite generating lower forces, will have greater accelerations and match distances. Deviations from this model are often suggestive of some type of elastic mechanism, allowing larger animals to maintain performance through the use of stored energy (Deban and O'Reilly, 2005).

MATERIALS AND METHODS

Twenty individuals of *D. ocoee* representing a full ontogenetic series (snout–vent length [SVL] 2.4–5.2 cm, mean: 3.3±0.87) were collected from Highlands, NC, USA. Salamanders were marked with three white paper discs, placed on the dorsal surface approximating the pectoral girdle, pelvic girdle, and one point halfway between the two girdles (Fig. 1). No glue was required, the moist skin of the salamanders adhered the discs to the skin. Individuals were encouraged to jump five times over a five cm gap by tapping metal forceps directly behind the individual, to simulate an approaching predator. The five cm gap exceeded maximum jumping performance in preliminary observations, and so was used to encourage maximum effort. Jumps were filmed from a dorsal view at 1000 frames/sec using a Photron FastCam high speed camera system (Photron USA Inc., San Diego, CA). Kinematic variables were measured using MaxTraq software (Innovision Systems Inc., Columbiaville, MI) for kinematics. Eight variables were analyzed for kinematics and scaling relationships: (1) direction of body bend, (2) angle of bending, (3) duration of bending (time to bend from initiation of bending to the time bending stopped), (4) duration of unbending (from initiation of unbending until body is straight), (5) duration of jump (amount of time from when all four limbs leave the surface

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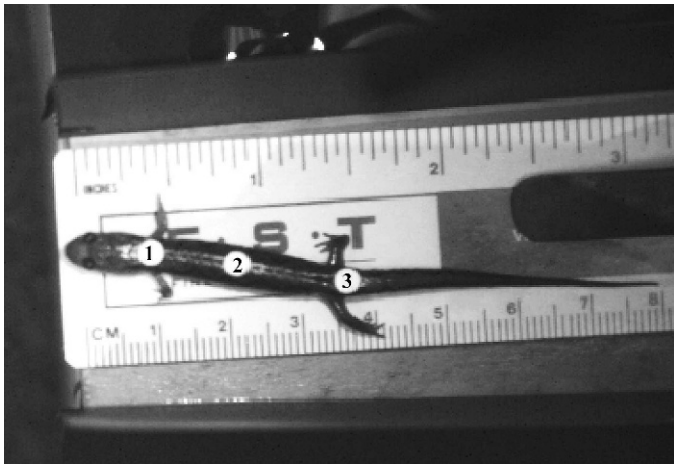
Fig. 1. Individual *D. ocoee* with landmarks for digital analysis with scale. Point 1 indicates the pectoral girdle, point 3 is the pelvic girdle, and point 2 is equidistant between the two girdles.

until one limb touches on landing on opposite platform), (6) jump distance (measured from right hind limb starting position to right hind limb landing position), (7) angular velocity of bending, and (8) angular velocity of unbending. Angles were measured from the pectoral and pelvic girdles, with their midpoint serving as the vertex. Initial observations indicated that lateral bending of the torso is the driving force behind this behavior; therefore, I focused on the variables that best describe this behavior. Individual mean jump values were used for analysis. For scaling relationships, angle of bending, durations and velocities were regressed against SVL. SigmaPlot software (Systat Software, Chicago, IL) was used for all statistical tests. Slopes were compared to one to determine scaling relationship against body length (Hill, 1950). T-tests were used for comparison of velocity variables. A chi-square test was used to test for preference of bend direction across all individuals. For all tests, $P < 0.05$ was considered statistically significant and no assumptions of the test were violated (normality, equal variance).

RESULTS

Desmognathus ocoee utilizes axial bending to propel jumping by laterally bending their body along one side, moving the anterior portion of the body toward the tail, and then rapidly straightening the torso (Fig. 2). This rapid movement propels the salamander into the air for total jump duration, from bending to completion, lasting less than 500 milliseconds (Table 1). There was no preference for a bend direction among individuals ($\chi^2 = 0.053$, df = 1, $P > 0.05$). Analysis of the scaling of the kinematic variables found jump duration, unbending velocity, and jump distance to be significantly different from expected isometry (Table 1). However, only bend duration, total duration, and bend velocity had any significant relationship with SVL (Table 1). Bending velocities and jump distance, critical measurements of performance, showed large amounts of

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Fig. 2. Representative image sequence of jumping in the salamander, *D. ocoee*. Numbers in the left corner correspond to time, in milliseconds.
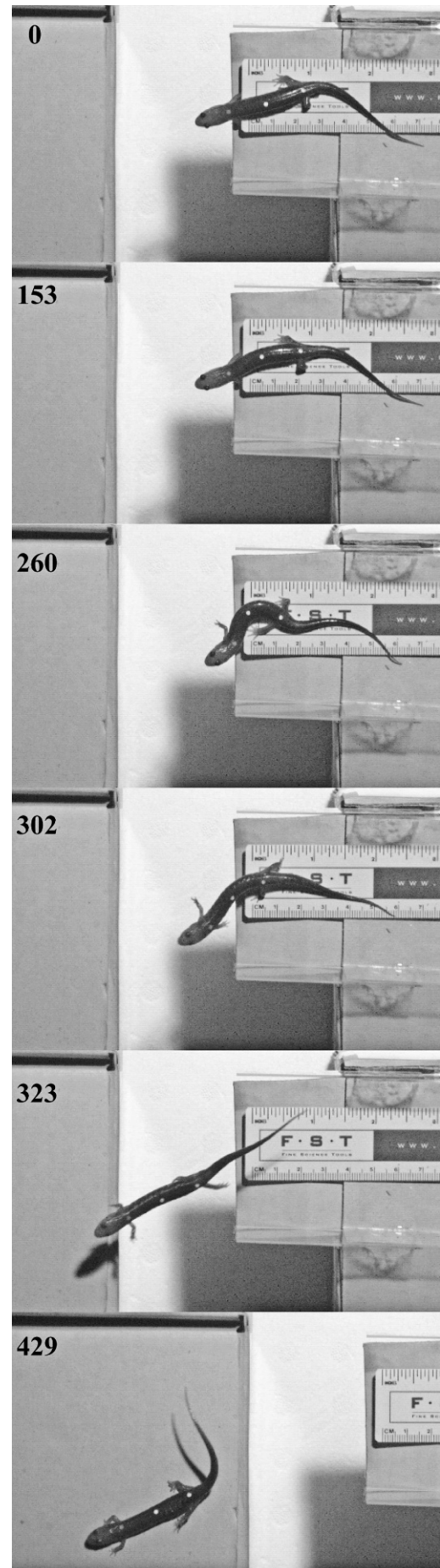
Table 1. Means, Regression Slopes, and Predicted Slopes of Isometry Describing the Jumping Behavior in *Desmognathus ocoee*. Isometric slopes were predicted using the relationships described by Hill (1950). Slopes marked with an asterisk indicate values that were different from zero. Isometry values marked with a superscript "a" indicate slopes that differed from predicted isometry.

Variable	Mean±SD	Reg. Slope±CI	Isometry
Bend duration (s)	0.13±0.06	0.894±0.81*	1
Unbend duration (s)	0.04±0.01	0.56±0.67	1
Jump duration (s)	0.07±0.02	0.05±0.52	1
Total duration (s)	0.25±0.07	0.53±0.48*	1
Bend angle (deg)	41.85±13.85	0.46±0.67	0
Bend velocity (deg/s)	432.06±277.87	−0.57±0.47*	−1
Unbend velocity (deg/s)	1216.74±591.8	−0.25±1.05	−1[a]
Jump distance (cm)	5.12±0.2	0.04±0.07	1[a]

variation (Fig. 3). Across the size range measured, unbending duration was lower than bending duration (Unbending [U]: 0.04±0.01 s, Bending [B]: 0.07±0.02 s, t = 7.35, P < 0.001), and unbending velocity was higher than bending velocity (U: 1216.74±591.8 deg/s, B: 432.06±277.87 deg/s, t = 7.65, P < 0.001).

DISCUSSION

The salamander *Desmognathus ocoee* jumps through the use of axial bending. Jumping is accomplished by bending of the body into a U-shape, followed by rapid straightening of the body. This provides the momentum necessary for the salamander to leave the ground and subsequently travel an indeterminate distance in the air, all within the span of less than a second. The role of axial musculature in salamander locomotion is well documented, primarily its use in walking and swimming (Frolich and Biewener, 1992; O'Reilly et al., 2000; Bennett et al., 2001; Azizi and Horton, 2004). Given the layering of salamander axial musculature and the differing fiber angles of each layer (Schilling and Deban, 2010) it remains to be seen which axial muscles are driving the jumping. Both the epaxial and hypaxial muscle groups are active during locomotion in *Ambystoma maculatum*, contributing to the lateral bending in both the terrestrial and aquatic environments (Deban and Schilling, 2009). In addition, the axial muscles are segmented throughout the trunk by myosepta, connective tissue, attaching to the transverse processes and neural spines of the vertebrae (Schilling and Deban, 2010). These myosepta may serve a role as an elastic recoil mechanism, discussed later.

Salamander jumping exhibits similarities to the C-start escape mechanism of aquatic vertebrates. Rapid lateral bending of the body in fishes increases acceleration of initial movements and the likelihood of escape (Domenici and Blake, 1997). While this has been best documented in fully aquatic fish in water (Weihs, 1973; Eaton et al., 1977; Domenici and Blake, 1997), aquatic and amphibious fish also rely on axial musculature to escape predation in the terrestrial environment (Swanson and Gibb, 2004; Gibb et al., 2011). Interestingly, there are some striking kinematic differences depending on the fish species. In the case of some amphibious blennies, the tail is moved toward the head (Hsieh, 2010), while the fully aquatic killifish moves the head toward the tail (Gibb et al., 2011). This may seem a trivial difference, but may be relevant in this discussion of salamander jumping. The amphibious blennies bend parallel to the surface plane, the tail is rotated to maximize the surface in contact with the surface. Conversely, the killifish

bends vertically, using gravitation forces to potentially store elastic energy in the axial musculature and skeleton (Gibb et al., 2011). Gibb et al. (2011) suggest that moving the center of mass increases the effectiveness of the "spring" motion during jumping in the killifish. These fish may serve as a useful comparison for jumping in *D. ocoee*, but the variety of kinematically distinct behaviors despite anatomical similarity in the fish preclude any discussions whether this terrestrial locomotion is a homologous behavior.

Examination of the scaling of jumping found few significant relationships with size. Traditionally, weak and missing scaling patterns were associated with elastic storage mechanisms. For many amphibians, elastic storage allows individuals of different sizes to maintain performance (Reilly, 1995; Deban and O'Reilly, 2005). In the case of hellbenders (*Cryptobranchus alleganiensis*), feeding requires rapid movements of the jaw and hyoid apparatus to create maximum suction for prey capture. Maintaining performance across a large size range is crucial for capture elusive prey, and it is unclear what properties of motor patterns, muscle architecture, and contractile elements allow hellbenders to maintain rapid jaw and hyoid movements (Deban and O'Reilly, 2005). With fire salamanders, (*Salamandra salamandra*), larvae also exhibited few patterns in the scaling of aquatic feeding, the mechanism is also unclear (Reilly, 1995). In the case of jumping *D. ocoee,* the putative elastic mechanism is similarly less obvious. There are no obvious tendons or catch mechanisms in the axial musculature or skeleton that would serve as the storage mechanism. However, between the segments of axial musculature are bands of connective tissue, the myosepta. The axial myosepta may be serving as the elastic storage mechanism. In the killifish jumping terrestrially, it is suggested that a pause between Stage 1 and Stage 2 of the jump could be the result of muscle activation and loading of elastic tissue. In the jumping of *D. ocoee*, this may also be true. Contralateral activation of the axial muscles while the salamander bends would allow for maximum tension prior to the jump. Contralateral activation is already known to occur during the stance phase of terrestrial locomotion, with the hypothesis that doing so retains tension within the trunk (O'Reilly et al., 2000). Integrating contralateral activation with multiple layered axial muscles during jumping may result in the rapid straightening of the salamander. This would allow larger salamanders to generate sufficient force to propel their bodies through the air without sacrificing performance, effectively acting as a spring mechanism. Jumping is an important defense mechanism in these salamanders (Brodie, 1977). For the smaller species, jumping
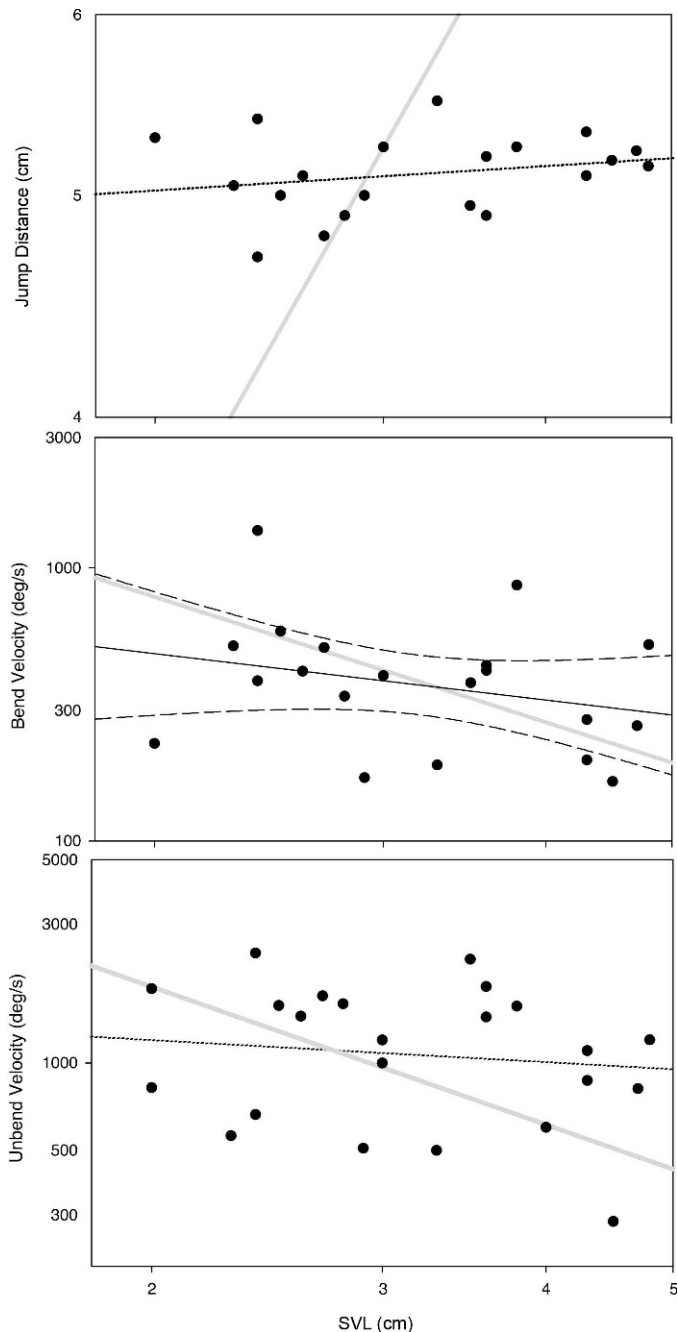
Fig. 3. Bivariate plots with log axes to examine scaling relationships in three variables: Jump Distance, Bend Velocity, and Unbend Velocity. Gray lines are lines of isometry, as dictated by Hill (1950). Bend Velocity was the only variable with a significant scaling relationship. The solid black line is the slope of the regression, and the dashed lines indicate 95% confidence intervals for that slope. For Jump Distance and Unbend Velocity, the dotted line indicates the slope of the line that best fits the relationship.

provides a means of escape from other salamanders that may be potential predators. For the larger species, snakes and birds are the primary predators, and the ability to jump rapidly will still serve as a viable defense mechanism (Brodie, 1977). However, larvae were only observed twice with a two-fold change in size, limiting the implications of the scaling relationship. While I observed multiple *D. ocoee* through a complete ontogenetic series, this still only represents a two-fold change in size.

This study represents the first kinematic investigation of jumping behavior of plethodontid salamanders, as well as the scaling properties of this behavior. The jump of *Desmognathus ocoee* resembles the C-starts seen in fishes. Both behaviors are powered by the contraction of axial musculature. However, in the case of the salamander, further investigation is needed into the role of the limbs and tail in this behavior. In anoles, the tail does not contribute actively to propelling the individual during a jump. However, loss of the tail has severe detrimental impacts on the stability of the anole during jumping (Gillis et al., 2009). *Desmognathus ocoee* will also autotomize the tail as a defensive behavior (Brodie, 1977), and I predict that a similar loss of stability will occur. Additionally, it remains to be seen how ubiquitous this behavior is within Plethodontidae. In addition to this work, there is anecdotal evidence of jumping in *Plethodon cinereus*, but no other species' jumping behavior has been reported (Murphy, 1917). One of the immediate next steps will be to examine the other members of *Desmognathus* and *Plethodon* for this jumping behavior, and potentially what limits size and shape play in this behavior.

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