

# Jumping in arboreal salamanders: A possible tradeoff between takeoff velocity and in-air posture

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## ABSTRACT

Jumping performance can have important implications for an animal's fitness by expanding its ability to evade predators and move between microhabitats. Jumping in terrestrial plethodontid salamanders is achieved through lateral bending and rapid unbending of the trunk, an action powered by axial musculature. Arboreal plethodontids, some of which are known to occupy tree crowns, tend to have more robust limbs and longer digits, which may affect their jumping kinematics and performance. We examined jumping kinematics in ten species of plethodontid salamanders, including four arboreal species of the genus *Aneides*, using high speed imaging and kinematic analysis. Salamanders of the genus *Aneides* exhibit lower takeoff velocities when compared with the terrestrial plethodontids *Eurycea*, *Desmognathus*, and *Plethodon*, possibly due to reduced trunk bending. *Aneides* also exhibit higher frequencies of two-footed takeoffs, and often orient their feet to launch from vertical surfaces when presented with the option. This suggests an alternative jumping behavior in salamanders that may reflect an arboreal lifestyle. All plethodontid species examined displayed distinctive in-air parachute postures after 45–100% of descending jumps, with *Aneides* showing the highest frequency of this behavior.

## 1. Introduction

Jumping is a common form of locomotion that modern tetrapods use for functions including movement among microhabitats, prey capture, and predator evasion (Alexander & Vernon, 1975; Emerson, 1985; Marsh, 1994; Hsieh, 2010; Gibb et al., 2011; McGowan & Collins, 2018). Many forms of jumping have been described; in most cases, jumps are powered by a pair of rapidly extending limbs, specifically the hind limbs for most vertebrate quadrupeds (Biewener, 2003). Several species of mammals jump by rapidly extending their hindlimbs and many store elastic energy for this behavior in the tendons of the hindlimbs, specifically the gastrocnemius and plantaris tendons (domestic cat [Harris & Steudel, 2002]; dog [Alexander, 1974]; hare [Carrier, 1995]; kangaroo rat [Biewener et al., 2009]; bushbaby [Aerts, 1998]; kangaroo [Alexander & Vernon, 1975]). A number of reptilian quadrupeds are also known to jump via limb propulsion (green anole [Bels et al., 1992]; Caribbean anoles [Losos, 1990; Toro et al., 2004]; and skinks [Goodman, 2007]), and the length of the hindlimbs has been found to influence jump performance [Toro et al., 2004]. Anurans are a diverse group including many avid jumpers in which function or performance have been examined (edible frog [Nauwelaerts & Aerts, 2006]; Australian rocket frog [James & Wilson, 2008]; spring peeper [Zug, 1972]; green frog [Zug, 1972]; northern leopard frog [Astley &

Roberts, 2014]; cane toad [Zug, 1972; Cox & Gillis, 2015]; Fowler's toad [John-Alder & Morin, 1990]; common toad [Goater et al., 1993]). Variation in jumping performance and hindlimb morphology in this group is attributed to ecological diversification (Gomes et al., 2009). Plethodontid salamanders exhibit substantial ecological diversification, but how this relates to jumping performance has not been described.

Unlike other legged vertebrates, terrestrial plethodontid salamanders jump by lateral bending and rapid propagation of the bend towards the tail, an action that is powered by axial musculature and works like a C-start in fishes (Ryerson, 2013; Ryerson et al., 2016; Hessel & Nishikawa, 2017). Many of the examined terrestrial plethodontids are capable of climbing, with at least 45% of non-permanently aquatic plethodontids reportedly climbing plants (McEntire, 2016). Little is understood about the degree of arboreality of many plethodontids, but for those that do climb and occupy arboreal niches, jumping could be an efficient approach to descend in response to environmental or predatory cues. Scansorial plethodontids, some of which are known to utilize arboreal habitats and elevated niches (Van Denburgh, 1916; Leonard, 1993; Spickler et al., 2006; McEntire, 2016), often have longer limbs and digits compared with more fossorial plethodontids (Stebbins, 2003; Petranksa, 2010). Given these differences in morphology and habitat use from more fossorial plethodontids, it stands to reason that arboreal plethodontids may differ in jumping

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behavior and performance.

*Aneides*, a scansorial and arboreal genus of plethodontid salamander, is known to utilize elevated niches including tree canopies, snags and stumps, and crevices of rocky outcrops (Stebbins, 2003). *Aneides vagrans* is known to occupy the crowns of the world's tallest trees, with sightings of individuals up to 88 m off the forest floor (Spickler et al., 2006). Its relatively long limbs and digits likely contribute to its impressive climbing abilities (Stebbins, 2003; Petranka, 2010) and theoretical models predict that quadrupeds with relatively long hindlimbs

should exhibit high takeoff velocities and jump farther (Alexander, 1968; Bennet-Clark, 1977; Emerson, 1985; Harris and Steudel, 2002). We therefore examined jumping in *Aneides* to determine if these features play a role in its jumping behavior and performance. We hypothesized that the hind limbs play an active role in jumping in *Aneides*. Jumping has been described in three other genera of plethodontid salamanders—*Desmognathus*, *Plethodon*, and *Eurycea*—among which no significant differences in kinematics or jumping performance have been found (Ryerson et al., 2016; Hessel et al., 2017). Given the striking differences in habitat use and hindlimb morphology, and the influence these factors have on jumping performance in other herpetofauna, we examined jumping in four species of *Aneides* to determine if they differ in kinematics compared with other jumping plethodontids.

## 2. Methods

We captured salamanders from a variety of localities across the continental United States, working with state and local wildlife agencies to establish collection sites. We used a cooler and icepacks to transport salamanders in plastic pint deli containers with unbleached, moistened paper towels and small holes in the lids. Animals were housed in the laboratory at the University of South Florida at 18 °C on a 12:12 h light cycle. Animals were housed on unbleached, moistened paper towels in covered plastic shoeboxes measuring 30 × 15 × 10 cm. Paper towels were replaced as needed and were never allowed to dry completely. Animals were fed a mix of small roaches and crickets once weekly and were checked daily for mortality and obvious signs of distress such as lethargy, thrashing, emaciation, lesions, and dryness.

We examined jumping kinematics in *Aneides aeneus* (N = 5), *Aneides flavipunctatus* (N = 4), *Aneides lugubris* (N = 4), *Aneides vagrans* (N = 5), *Desmognathus aeneus* (N = 5), *Desmognathus ocoee* (N = 5), *Desmognathus quadramaculatus* (N = 5), *Eurycea guttolineata* (N = 3), *Eurycea wilderae* (N = 5), and *Plethodon metcalfi* (N = 5) using high speed imaging and kinematic analysis. Several additional species, listed below, including a few species outside family Plethodontidae, were investigated but not utilized in this experiment for apparent lack of jumping abilities. We used an Edgetronic SC1 high-speed camera with a 105 mm Nikon lens (Supplemental Videos S1–S7) and a mirror angled at 45 degrees to image salamander jumps at 500 Hz in dorsal and lateral view. We imaged a total of 230 successful jumps from 46 individuals representing 10 species across four genera of Plethodontidae (Table 3).

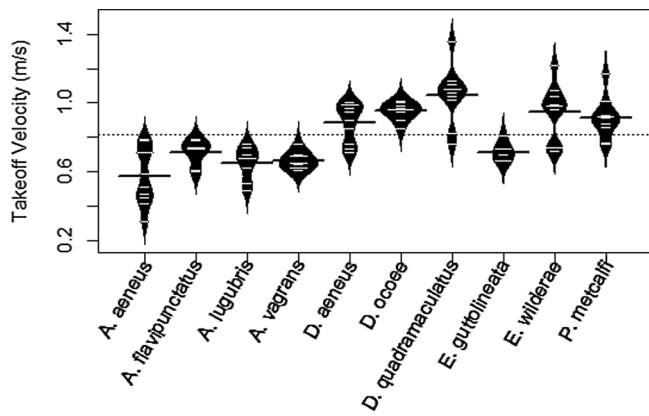
Animals were encouraged to jump after being placed near the end of a wooden plank hanging 75 mm above a foam landing pad. For *Desmognathus quadramaculatus* only we removed the wooden plank and created a broader surface, still 75 mm above a foam landing pad, because *D. quadramaculatus* was more cooperative under these conditions. Successful jumps were defined as jumps in which the animal's foot did not slip and the body and tail did not drag against the launch-surface during takeoff (Supplemental Videos S1–S7); unsuccessful jumps were defined as trials in which the animal's foot slipped (Supplemental Videos S8–S9) or the animal's tail or body dragged against the launch-surface (Supplemental Videos S10–S11) influencing takeoff velocity. All jumps were recorded at an ambient temperature of 18 °C and ambient humidity ranging from 55–70%. All individuals were given at least five

minutes of rest between jumps and no individuals were made to jump more than three times per day. Jumping in some individuals occurred spontaneously (Supplemental Video S5); jumping in others was elicited by tapping a metal utensil on the wood behind them to simulate danger (Supplemental Video S6). Salamanders were given a shaded area to aim for, which encouraged jumps parallel to the lateral image plane, and 5 mm grid paper was taped to the launch and landing surfaces for scale. Animals that did not jump after fifteen minutes of coaxing on three separate days were classified as non-jumpers, and species with three consecutive non-jumping individuals were classified as non-jumping species for the purposes of this study.

ImageJ software (National Institutes of Health, Bethesda, Maryland, USA; Rasband, 2018) was used to calculate kinematic variables such as bend angle, unbend velocity, number of feet used during takeoff, orientation of takeoff surface (vertical or horizontal), and time to assume a parachute posture. Bend angle was calculated from the dorsal-view images using the angle tool in ImageJ and connecting points along the center of the dorsum at the pectoral girdle, midway between the appendicular girdles, and the pelvic girdle; all bend angles were subtracted from 180 such that 0° represents a straight trunk and larger numbers reflect more extreme bending. Unbend velocity was calculated by dividing the bend angle by the time it took for a salamander's body to unbend to 0°. The x, y coordinates of a fixed anatomical point approximating the location of the center of mass, midway between the pectoral and pelvic girdles were recorded for each frame of the video sequences at the time of takeoff using the point tool in ImageJ; we used the series of x, y coordinates from each jump to calculate average and maximum jump velocity, acceleration, and power smoothed with a cubic spline. The takeoff period began with the first frame that torso unbending was detected and ended at the first frame in which the salamander is making no contact with the jumping platform. We calculated the mean, standard deviation, and 95% confidence intervals for takeoff velocity by species and genera using the two trials with the highest performance from each individual. We compared jump performance, using takeoff velocity as our response variable, between species and genera using ANOVA and Tukey HSD multiple comparison procedure. We noted the frequency of two-footed takeoffs and orientation of takeoff surface and logit-transformed that frequency data to compare between species. We also noted the frequency at which salamanders achieved a prone, "parachute posture" while falling. Parachute posture was defined as having been achieved when a salamander displayed parasagittal extension of the vertebral column and abducted all four limbs so that they were maintained perpendicular to the trunk (Fig. 6). We calculated the time from launch to parachute posture when applicable; average time from launch to parachute was compared between genera using ANOVA/Tukey Test.

## 3. Results

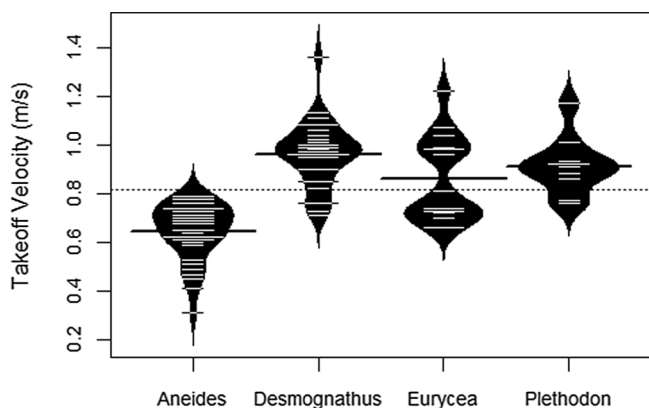
Jumping in all four species of *Aneides* followed the same general sequence. The salamander positioned itself at the end of the jumping platform, typically dangling the head, forelimbs, and anterior half of the trunk over the edge of the platform (Fig. 6A). The jump was initiated with a parasagittal extension of the head immediately followed by a rapid unbending of the trunk; the unbending of the trunk occurred while the head continues to extend parasagittally (Fig. 6B). The rapid unbending of the trunk propelled the salamander horizontally; as the body of the salamander began to move horizontally the forelimbs, and usually one of the hindlimbs, were rapidly abducted leaving a single hindlimb on the jumping platform (Fig. 6C). The jump was completed when the salamander's last foot left the substrate with the remaining hindlimb(s) and continued horizontally through the air, usually abducting the final hindlimb(s) to achieve a controlled parachute posture (Fig. 6D). The kinematics of jumping in *D. ocoee* appeared to be consistent with previous observations (Ryerson, 2013). The kinematics of jumping in *D. aeneus* and *D. quadramaculatus* appeared to be similar to



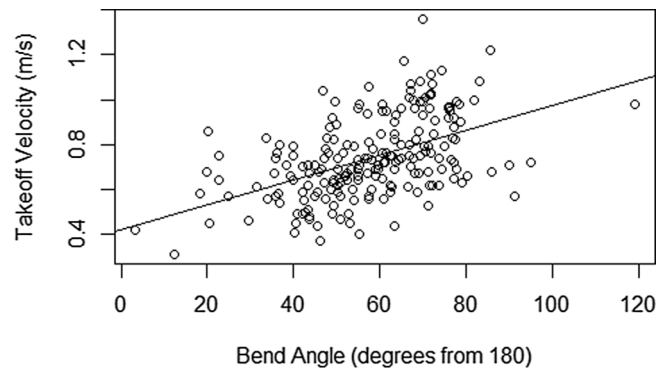
**Fig. 1.** Bean plots of takeoff velocity for 10 species of plethodontid salamander. Bean shape is given by a normal density trace and its mirrored version. Black lines represent the mean takeoff velocity for each species; white lines represent actual takeoff velocities, with wider white lines indicating multiple jumps with roughly the same takeoff velocity. The horizontal, dashed line represents the overall average for all species. Bean height represents  $\pm 3$  standard deviations from the mean.

that of *D. fuscus* and *D. ochrophaeus*, the kinematics of jumping in *E. guttolineata* and *E. wilderae* appeared to be similar to that of *E. bislineata* and *E. longicauda*, and jumping in *P. metcalffi* appeared is similar to that of *P. cinerus* and *P. glutinosus* (Ryerson et al., 2016).

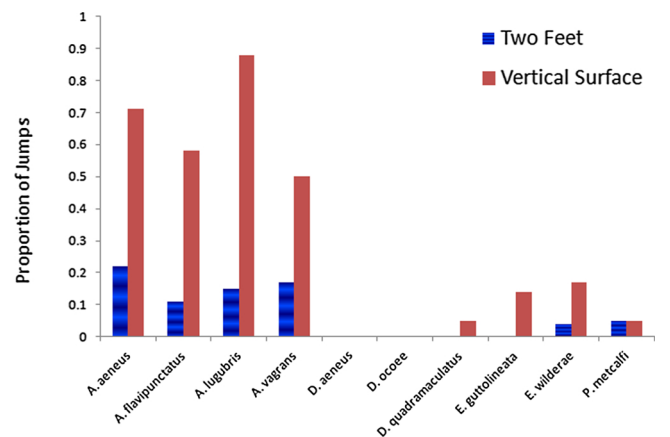
No significant differences in jump performance were detected between individuals of the same species. Takeoff velocity is significantly lower in *Aneides* compared to other plethodontids ( $F = 22.04$ ,  $df = 3$ ,  $p < 0.001$ ; Figs. 1 and 2). A significant relationship was detected between takeoff velocity and bend angle when analyzing all jumps regardless of species ( $F = 45.28$ ,  $df = 224$ ,  $p < 0.001$ ; Fig. 3). The frequency with which *Aneides* launched using two feet is significantly higher than that of other plethodontids ( $F = 4.949$ ,  $df = 3$ ,  $p = 0.006$ ), and *Aneides* used vertically-oriented takeoff surfaces with greater frequency than all other species tested except *E. guttolineata* ( $p < 0.001$ ; Fig. 4). All species in the genus *Aneides* exhibited frequent take-offs from vertical launch surfaces, pushing off against the end of the wooden plank (Fig. 4). *Aneides* exhibited higher frequencies of prone, parachute posture during falling and achieved those postures more quickly than other plethodontids ( $F = 7.87$ ,  $df = 3$ ,  $p < 0.001$ ; Table 2; Fig. 5), although all species that jumped exhibited parachute postures in



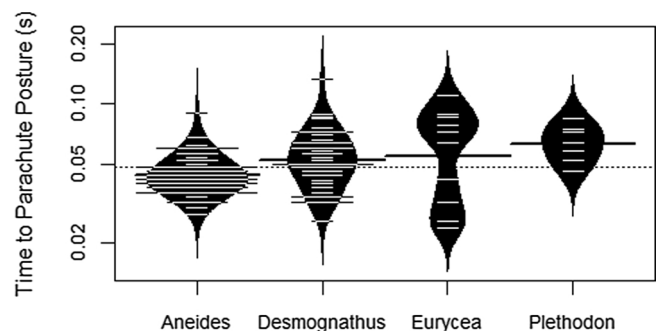
**Fig. 2.** Bean plots of takeoff velocity for 4 genera of plethodontid salamander. Bean shape is given by a normal density trace and its mirrored version. Black lines represent the mean takeoff velocity for each genus; white lines represent actual takeoff velocities, with wider white lines indicating multiple jumps with roughly the same takeoff velocity. The horizontal, dashed line represents the overall average for all genera. Bean height represents  $\pm 3$  standard deviations from the mean.



**Fig. 3.** Takeoff velocity as it relates to degree of lateral bending in plethodontid salamanders (Adj  $R^2 = 0.24$ ,  $df = 224$ ,  $p < 0.001$ ). All takeoff velocities were calculated by tracking the center of mass of the salamanders in ImageJ. Higher bend angles above reflect more lateral bending before a jump while lower bend angles reflect less lateral bending before a jump.



**Fig. 4.** Proportion of jumps exhibiting a newly described jumping form, measured by the frequency of launches using both hind feet (blue, striped bars) and vertical launch surfaces (red, non-striped bars).

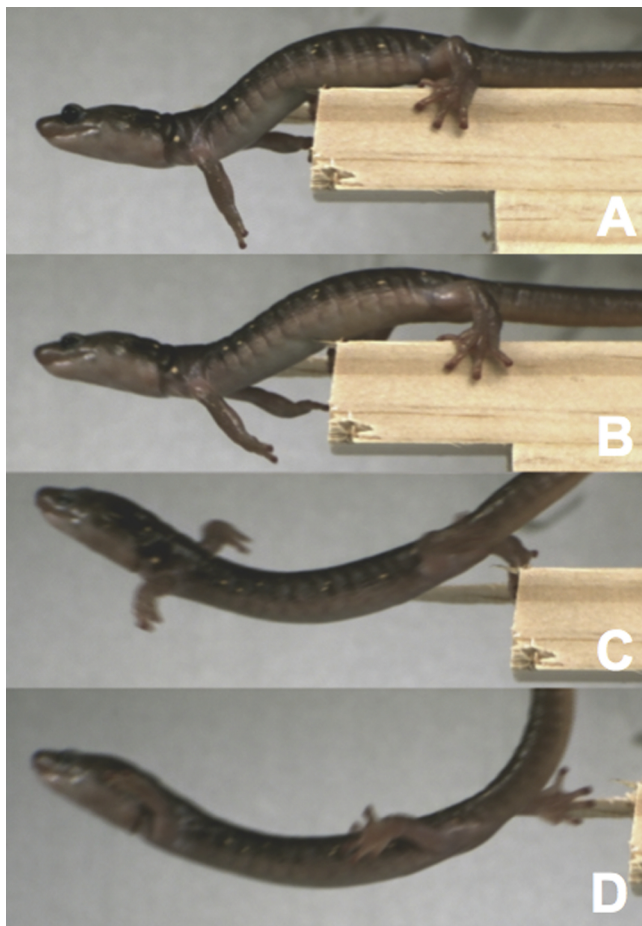


**Fig. 5.** Bean plots of time from launch to parachute posture during a jump for four genera of plethodontid salamander. Bean shape is given by a normal density trace and its mirrored version. Black lines represent the mean time to parachute posture for each genus; white lines represent actual times to parachute posture, with wider white lines indicating multiple jumps with roughly the same time to parachute posture. The horizontal, dashed line represents the overall average for all genera. Bean height represents  $\pm 3$  standard deviations from the mean.

45%–100% of descending jumps.

Species in family Plethodontidae that did not jump include *Ensatina eschscholtzii*, *Plethodon elongatus*, *Gyrinophilus porphyriticus*, and *Bolitoglossa franklini*. Non-jumping species in other families of salamander included *Dicamptodon tenebrosus*, *Ambystoma gracile*, and *Ambystoma maculatum*.





**Fig. 6.** Parachute posture (panel D) of *Aneides lugubris* defined by a parasagittal extension of the vertebral column, a lack of lateral trunk bending, and the abduction of all four limbs so that they maintain a position perpendicular to the trunk.

#### 4. Discussion

Despite using both hind limbs more during takeoff, *Aneides* exhibited poor jumping performance compared with the other, more fossorial plethodontids. This could be due to reduced lateral bending observed before jumps (Table 1), with more extreme bending found to be correlated with higher takeoff velocities (Fig. 3). We posit that any jump resulting in free-fall from an elevated niche is sufficient to evade

**Table 1**

Kinematics of plethodontid salamander jumps using the top two recorded jumps from each individual (N = 3–5 individuals per species, depending on availability). Bend angle and takeoff velocity include  $\pm 1$  standard deviation; frequency of launches using both hind limbs (Two Feet) and frequency of launches from a vertical surface (Vertical Surface) were recorded (Fig. 4).

Species	N	Bend Angle (deg)	Takeoff Velocity (m/s)	Two Feet	Vertical Surface
<i>A. aeneus</i>	5	36.5 $\pm$ 10.0	0.57 $\pm$ 0.17	0.22	0.71
<i>A. flavipunctatus</i>	4	55.0 $\pm$ 7.9	0.72 $\pm$ 0.07	0.11	0.58
<i>A. lugubris</i>	4	43.5 $\pm$ 11.3	0.65 $\pm$ 0.10	0.15	0.88
<i>A. vagrans</i>	5	50.4 $\pm$ 9.8	0.66 $\pm$ 0.05	0.17	0.50
<i>D. aeneus</i>	5	69.8 $\pm$ 7.6	0.89 $\pm$ 0.11	0	0
<i>D. ocoee</i>	5	71.2 $\pm$ 7.8	0.95 $\pm$ 0.05	0	0
<i>D. quadramaculatus</i>	5	67.4 $\pm$ 12.2	1.05 $\pm$ 0.19	0	0.05
<i>E. guttolineata</i>	3	48.1 $\pm$ 5.9	0.72 $\pm$ 0.06	0	0.14
<i>E. wilderae</i>	5	61.8 $\pm$ 23.0	0.94 $\pm$ 0.16	0.04	0.17
<i>P. metcalfi</i>	5	52.6 $\pm$ 16.5	0.91 $\pm$ 0.13	0.05	0.05

**Table 2**

Frequency (%) and rate at which various species of plethodontid salamander achieved a parachute posture after a jump from 75 mm.

Species	Parachute Frequency	Avg Time to Parachute (s)
<i>A. aeneus</i>	100	0.043
<i>A. flavipunctatus</i>	88	0.047
<i>A. lugubris</i>	100	0.040
<i>A. vagrans</i>	89	0.044
<i>D. aeneus</i>	68	0.051
<i>D. ocoee</i>	73	0.058
<i>D. quadramaculatus</i>	45	0.060
<i>E. guttolineata</i>	57	0.071
<i>E. wilderae</i>	61	0.062
<i>P. metcalfi</i>	75	0.064

**Table 3**

Average mass, average snout-vent length (SVL), and average total length (Total) of jumping species of plethodontid salamander. Sample size (N) for each species is shown.

Species	N	Mass (g)	SVL (mm)	Total (mm)
<i>A. aeneus</i>	5	3.32	46	79
<i>A. flavipunctatus</i>	4	3.58	55	102
<i>A. lugubris</i>	4	9.36	80	152
<i>A. vagrans</i>	5	3.70	62	107
<i>D. aeneus</i>	5	0.56	29	52
<i>D. ocoee</i>	5	1.82	45	88
<i>D. quadramaculatus</i>	5	7.08	69	129
<i>E. guttolineata</i>	3	0.87	37	89
<i>E. wilderae</i>	5	0.62	36	83
<i>P. metcalfi</i>	5	5.46	68	128

predation, thus it is possible that there exists little selection pressure for high performance takeoff velocities in natural populations of *Aneides*.

The tendency to use a vertical launch surface could indicate that arboreal plethodontids prefer to jump only once they have run out of other viable options (i.e., jumping is a secondary or tertiary form of predator evasion). During laboratory trials, individuals of *Aneides* were especially reluctant to jump and would try turning around, climbing upward, and dangling the anterior half of their trunk over the wooden plank while waving their forelimbs in a rostroventral direction before resorting to jumping. Alternatively, toeing-off from a vertical surface could initiate a quicker falling-escape with reduced risk of dragging against a horizontal launch surface. It is worth noting that 100% of two-foot takeoffs in *Aneides* involved at least one foot toeing off from a vertical surface.

The strategy of launching from two feet does not result in increased takeoff velocity by *Aneides* and could simply be a result of having relatively longer limbs compared with the other plethodontids examined. It is also possible that this alternative to the plethodontid jumping behavior that has been reported, which involves a salamander pole-vaulting over a single planted hindlimb (Hessel & Nishikawa, 2017), results in a more prone body position during takeoff; *Aneides* achieved a prone, parachute posture after toe-off at higher frequencies and, on average, achieved those postures more quickly than other plethodontids (Table 2; Fig. 5). It is also worth noting that *Aneides* will not jump a gap as *Desmognathus fuscus*, *Desmognathus ochrophaeus*, *Plethodon cinerus*, *P. glutinosus*, *Eurycea bislineata*, and *E. longicauda* have been recorded doing (Ryerson, 2013; Ryerson et al., 2016; Hessel & Nishikawa, 2017); rather, they required a vertical descent before jumping, and appeared to carefully target points visually below before jumping. Two-foot takeoffs occurred only twice among all other species, once in *Eurycea wilderae* and once in *Plethodon metcalfi*, during which both feet toed-off from horizontal surfaces.

Imaging downward jumps to accommodate *Aneides* allows us to examine the frequencies at which jumping plethodontids achieve parachute postures during 75 mm descents, the speed with which they

achieve such postures, and whether these factors reflect an ability to direct their aerial descent as is seen in tetrapods with similar morphology (Jusufi et al., 2008; Jusufi et al., 2011).

Of the non-jumping species in the family Plethodontidae, we were most surprised by the reluctance of *Plethodon elongatus* to jump because they exhibit similar morphology to other species of *Plethodon* that are known to jump: *P. cineris* and *P. glutinosus* (Ryerson et al., 2016). Of the non-jumping species outside the family Plethodontidae, we were most surprised by the lack of jumping exhibited by *Dicamptodon tenebrosus*. Captive *D. tenebrosus* have been imaged leaping off the ground for earthworms (Morris, 2015) and we have observed jumping in *D. tenebrosus* during prey capture. Despite these known occurrences, we could not entice *D. tenebrosus* to jump evasively in this study and are unable to properly describe the behavior or kinematics of the feeding jumps.

Average maximal horizontal velocity of all plethodontid salamanders tested ( $0.75 \pm 0.18$  m/s) resembles that of Caribbean *Anolis* lizards ( $0.79 \pm 0.08$  m/s, Losos, 1990). However, salamander jump distance ( $< 25$  cm for all observed jumps) falls below the range of jump distances calculated for fifteen species of Caribbean *Anolis* lizards ( $27.7 \pm 1.46$  cm –  $97.0 \pm 2.73$  cm) despite salamanders jumping from a platform nearly three times as high. Similarly, jump distance in plethodontid salamanders is eclipsed by jump distances calculated for jumping anurans, many of which cover horizontal distances over 50 cm (Rand & Rand, 1966; Zug, 1972; Nauwelaerts & Aerts, 2006) and some of which cover horizontal distances over 100 cm with a single jump (James & Wilson, 2008). Plethodontid salamanders power their jumps with axial musculature and trunk extension and display lower jump capacity than other vertebrate quadrupeds that use hindlimb extension, and in some cases elastic recoil, to power their jumps.

## 5. Conclusions

Our research shows that arboreal salamanders of the genus *Aneides* utilize a previously undescribed jumping behavior, perhaps reflecting their use of elevated niches in nature. Specifically, *Aneides* exhibit reduced lateral bending, higher frequency of takeoffs using two hind feet instead of one, and often orient their feet to launch from vertical surfaces when presented with the option. In a laboratory setting, this form of jumping is associated with lower takeoff velocity, and therefore of reduced jump performance, compared with jumping performance of other plethodontid salamanders not known to occupy elevated niches. However, jumping could be equally effective for evading predators despite a lower takeoff velocity if the outcome is simply falling out of danger. All species tested exhibited parachute posture after jumping, which may serve to slow and direct their descent.

## Summary Statement

Jumping performance and behavior in an arboreal genus of salamander is described.

## Declaration of Competing Interest

None.

## Acknowledgements

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.zool.2019.125724>.

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