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Source: *Herpetologica*, 73(2):100-104.

Published By: The Herpetologists' League

<https://doi.org/10.1655/Herpetologica-D-15-00067.1>

URL: <http://www.bioone.org/doi/full/10.1655/Herpetologica-D-15-00067.1>

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## Doing Without: Jump Performance After Tail Autotomy in Three Species of Plethodontid Salamanders

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**ABSTRACT:** The ability of plethodontid salamanders to jump has been recognized for over 100 yr, but the mechanics of the jump are only now being elucidated. These salamanders often autotomize tails that can be as much as a third of the body mass. Tail loss alters jump performance in some lizards and therefore may also alter jump performance in the plethodontid salamanders. In this study, we used a high-speed camera to record subjects representing three species of plethodontid salamanders jumping with and without tails. The kinematic analyses indicate that take-off velocity, take-off angle, and maximum height are similar between salamanders with and without tails. Jump characteristics are highly variable within the individual for all salamanders (with or without tails) and this indicates that salamanders do not need to produce the same jump consistently to succeed in their primary task of escape. Better coordination might exist for arboreal plethodontid salamanders that use jumping for purposes other than escape. Future studies should focus on the in-air dynamics and landing kinematics of the salamander, as the tail plays a large role during in-air balance and landing control in other tetrapod species that jump.

**Key words:** Biomechanics; *Desmognathus*; Escape; Kinematics; *Plethodon*

TAIL AUTOTOMY is a common escape tactic found in many vertebrates, including rodents (Dubost and Gasc 1987), squamates (Clause and Calpaldi 2006; Bateman and Fleming 2009; McElroy and Bergmann 2013), and caudates (Wake and Dresner 1967; Maginnis 2006). In amphibians and reptiles, voluntary tail loss is a defense mechanism that diverts the predator's attention to the tail rather than the prey, allowing for escape (Brodie 1977; Vitt et al. 1977; Arnold 1984). For example, gecko tails will violently thrash around postseparation, tossing themselves several body lengths into the air in an attempt to divert the attention of predators (Higham and Russell 2010). Tail autotomy as an escape strategy has been directly observed in the field, where the attention of a predator (*Antechinus swainsonii*; Dusky Marsupial Mouse) was diverted to an autotomized tail, allowing for the prey (*Christinus marmoratus*, Marbled Geckos) to escape (Daniels et al. 1986). However, tail autotomy comes at a cost (Bateman and Fleming 2009); for example, the tail is commonly a storage organ for fat reserves, the loss of which can affect winter survival, reproduction rates, and future escape capabilities (Maginnis 2006). Furthermore, a loss of tail length can influence social status (Fox and Rostker 1982) and fecundity (Congdon et al. 1974).

The impacts of tail loss on locomotor performance vary widely in lizards (McElroy and Bergmann 2013; Gillis and Higham 2016). Tail autotomy can increase running speeds in some lizard species (e.g., *C. marmoratus* [Marbled Geckos; Daniels 1983], *Niveoscincus metallicus* [Metallic Cool-skinks; Chapple and Swain 2002]), decrease escape speeds in others (e.g., *Scincella lateralis* [Little Brown Skinks; Formanowicz et al. 1990]), or have no impact (e.g., *Lygodactylus capensis* [Cape Dwarf Geckos; Fleming and

Bateman 2012]). Tail loss results in an anterior shift of the center of mass that alters jumping mechanics in some lizards (Gillis et al. 2013). Additionally, once airborne, many lizards, including anoles (Gillis et al. 2009; Kuo et al. 2011; Gillis et al. 2013), agamids (Libby et al. 2012), and geckos (Jusuifi et al. 2008) use their tails for in-air stabilization and control.

Several species of Plethodontidae (lungless salamanders) jump using a rapid extension movement of the torso from a C-shaped lateral bending position (Kingsley 1884; Cochran 1911; Ryerson 2013). We recently characterized these jumps in detail for six species of plethodontid salamanders and found that although morphology differs between species, there were no differences in their jumping kinematics such as jump height, take-off angle, and take-off velocity (Ryerson et al. 2016). These salamanders employ tail autotomy as an escape strategy, but any impact on jump performance is unknown. It is unclear what contribution the tail makes during jumping because the tails of these salamanders are not highly muscular (compared to jumping lizards) or prehensile. However, salamander tails make up a significant proportion of the total body mass. During the take-off phase of the jump, the tail might function to balance the salamander or increase static friction of the hindfoot for better grip. To investigate the contribution of the tail to jump take-off, we focused on the jumping parameters of take-off velocity, take-off angle, and maximum jump height. We predicted that the salamander tail functions in some capacity during jump take-off. If true, we hypothesized that salamanders will show a reduced take-off velocity, take-off angle, and maximum jump height after tail loss.

### MATERIALS AND METHODS

We collected three species of plethodontid salamanders from the edges of streams and creeks within the Allegheny College Bousson Environmental Research Reserve (Meadville, Pennsylvania, USA): *Desmognathus fuscus* ( $n = 5$ , snout-vent length [SVL] = 3.6–5.5 cm), *Desmognathus ochrophaeus* ( $n = 5$ , SVL = 2.8–4.2 cm), and *Plethodon*

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*cinereus* ( $n = 5$ , SVL = 1.9–3.9 cm). We collected salamanders in late spring through early summer and then housed each salamander separately in plastic containers lined with wet paper towels at 16°C with a 14 : 10 h light : dark photoperiod. Feeding with *Drosophila melanogaster* occurred twice a week. Each salamander was photographed with a digital camera next to a ruler. The photograph files were imported into the digitizing freeware ImageJ (v1.4q, National Institutes of Health, Bethesda, MD) to measure SVL and tail length ( $\pm 0.01$  cm). We measured the body mass ( $\pm 0.001$  g) of each salamander immediately prior to its use in experimental trials.

Our jump arena was set up as described in Ryerson et al. (2016). Briefly, we filmed salamanders jumping at 500 frames/s with a Fastec Inline 1000 high-speed camera system (640 × 240 resolution at 500 Hz; Fastec Imaging Corporation) from lateral and dorsal perspectives simultaneously with the use of a mirror placed at a 45° angle above the jump arena. Within the arena, the objective for each subject was to jump across a 5-cm gap between two platforms. The first platform had a 5 cm wide by 30 cm long runway to guide the salamanders toward the second platform, which was placed 5 cm away and 10 cm below the first platform. We tapped a blunt object next to the salamander to encourage jumping. We defined successful jumps as those that matched Ryerson's (2013) description that the salamander bends into a C-shape and then rapidly straightens out, followed by limb take-off with no visible foot slippage. We recorded an initial bout of five jumps for each subject with  $\geq 5$  min of recovery period between jump attempts.

Following the initial jump trials, we removed salamander tails. In preparation for this portion of our study, we tried to coax the salamanders to autotomize their tails by tapping the tails with a blunt object, but were unsuccessful. We then attempted to simulate a predatory attack by grabbing their tail, but the relative length of tail detached varied between subjects. Therefore, to minimize stress on the salamanders and have a similar amount of tail loss among individuals, we anesthetized all salamanders with 0.01% tricaine methanesulfonate (MS222, Fisher Scientific International Inc.) and surgically removed their tails at the visible cleavage plane posterior of the cloaca. After a 2-d recovery period, we recorded the mass of each subject prior to a second bout of jumps. We again recorded jumps performed by these subjects, as described above, within 1 wk of tail amputation to minimize tail regrowth or learned compensation mechanisms. For each individual, we used five successful tailless trials for subsequent analysis. Following the jumping trials, we euthanized salamanders with 0.2% MS222.

We tracked the center of mass throughout the salamander jump with the use of a software application that incorporated Excel (v16.0, Microsoft Corporation, Redmond, WA) and Didge (v2.3, Alistair Cullum, Creighton University, Omaha, NE), as described in Hessel (2014) and Ryerson et al. (2016). Digital images of each subject were disarticulated into 10 segments: complete limbs (4), two equal-length torso segments (from pectoral girdle to pelvic girdle), two equal-length tail segments (anterior end of the first caudal vertebra to the end of the tail), the pelvis segment, and head segment. Immediately after each subject was euthanized, we used a scalpel to sever the specimen into these same segments and recorded the mass of each. On each video frame during a

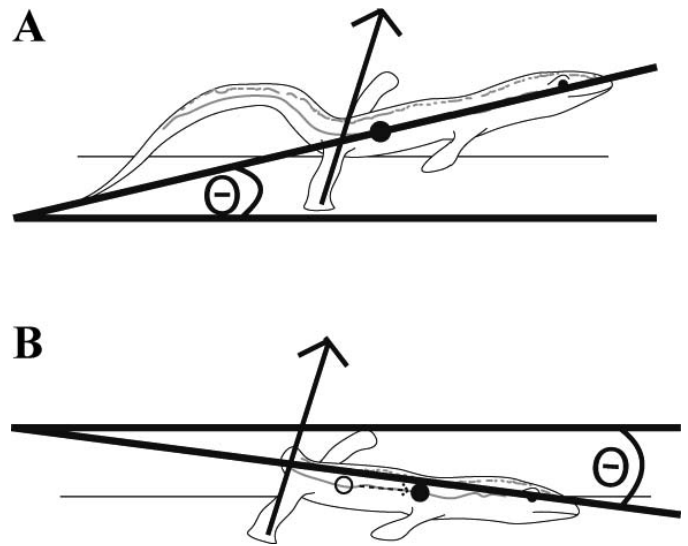


FIG. 1.—A representation of a jumping plethodontid salamander at take-off. The angle represented on the diagram ( $\theta$ ) is the take-off angle, and the arrow is the estimated ground reaction force produced by the hindlimb. Take-off is defined as the point at which the final hindlimb leaves the ground. (A) Typical jump; (B) a negative take-off angle, only observed in tailless salamanders, which still produces a jump.

jump, we manually digitized all segments with the use of the functions provided in Didge. This strategy allowed us to place each segment's center of mass throughout the jump consistently. Each segment was assumed to be cylindrical, and thus the segment's center of mass was placed at the halfway point along its longest axis. After digitization, all segment locations and masses were used to calculate the salamander's center of mass during the jump (Özkaya et al. 2012; Ryerson et al. 2016).

We measured take-off angle (degrees), take-off velocity (m/s), and maximum vertical jump height (cm). We defined take-off as the frame during which the last hindlimb left the ground. We defined take-off angle as that between the horizon and a line that intersected both the girdles (Fig. 1A), take-off velocity as the linear velocity of the center of mass at take-off, and maximum jump height as the maximum vertical height attained by the center of mass of the salamander while airborne, relative to the plane of the take-off platform. Negative take-off angles were the result of the hips of the salamander being above the pectoral girdle at take-off (Fig. 1B).

We used JMP Pro (v11.0, SAS Institute Inc., Cary, NC) for all statistical analyses. We prescreened the data and removed data points if they were more than two standard deviations away from the mean to limit skewing of the data (two jumps by tailed *D. fuscus*, and one jump by a tailless *P. cinereus*). We used a general linear model (GLM) analysis with species and tail status as fixed effects, tail status × species interaction effect, individual subject as a random effect (repeated measure), and individual subjects nested within species (using all trials from each subject, except those excluded to limit skewing). This GLM design was used to test each response variable (take-off velocity, take-off angle and maximum height) separately. In addition to running these analyses with the variables described, we also normalized take-off velocity and maximum height by subject

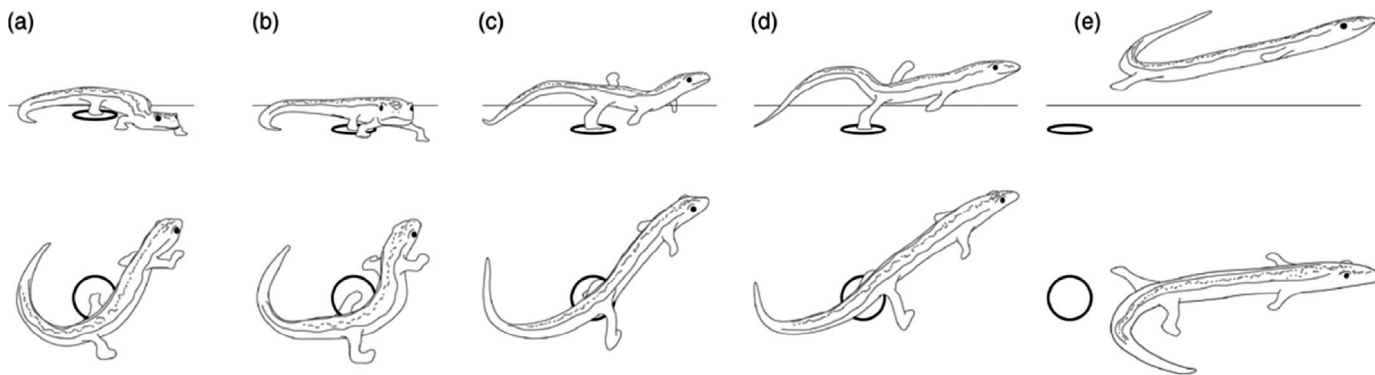


FIG. 2.—Line drawing of a representative jump by a plethodontid salamander. Top row, lateral view; bottom row, dorsal view. (a) Onset of bending, (b) maximum bending, (c) end of unbending, (d) last foot leaving the ground, (e) all limbs off the ground. Note: the subject leaves the substrate using the right and left hindlimb in the lateral and dorsal views, respectively. Figure adapted from Ryerson et al. (2016), with permission.

SVL, and performed the same GLMs to look for differences attributable to normalizing the data. We used post hoc Tukey honestly significant difference (HSD) analyses to detect differences between response means. We also screened significant interaction effects with a least-squares means plot, and performed an ordinary least-squares (OLS) linear regression analysis between maximum jump height and take-off angle for all recorded jump trials. A Type I error of  $\alpha = 0.05$  was used for all statistical tests; we report both the mean  $\pm 1$  SD and 95% confidence intervals (CI) for each response parameter.

RESULTS

The jump mechanics for tailed and tailless individuals were similar to those described in Ryerson (2013) and Ryerson et al. (2016). The jumps for each subject typically consisted of the salamander bending its torso into a “C” shape, followed by a noticeable pause (~5–20 ms). Then, a rapid unbending phase followed that consisted of simultaneous torso straightening and hindlimb push-off with a trajectory up and away from the jump platform (Fig. 2).

After tail removal, the salamanders lost  $26.39 \pm 9.98\%$  and  $47.76 \pm 5.03\%$  of their body mass and total length, respectively. The analyses of absolute and relative data for take-off velocity and maximum height yielded similar results, and so only the absolute data are discussed here (results for normalized variables can be found in Table S1, available online in the Supplemental Materials). For all subjects, take-off velocity, take-off angle, and maximum height values were variable from trial to trial as evidenced by the large standard deviations and 95% CI values in the pooled data (~30–60%

of mean). This variability did not change among subjects following tail loss (Table 1).

The GLM analyses detected an effect of species for take-off angle, while all other tests were insignificant (Table 2). The Tukey HSD analyses of take-off angle identified that, compared to the other two species, *D. fuscus* produced smaller jump angles, and *P. cinereus* produced larger jump angles, regardless of tail status. A post hoc least-square means plot analysis showed that *P. cinereus* and *D. ochrophaeus* least-square means were ~5% different from each other, and *D. fuscus* was ~20–25% smaller than the other two. These data indicate that *P. cinereus* and *D. ochrophaeus* are similar in respect to jump angle, and that *D. fuscus* jump at a smaller take-off angle.

When examining the range of take-off angle values, we found that nine jumps had negative take-off angle values (ranging from  $-0.8$  to  $-10.8$  degrees), and all occurred in tailless individuals across all three species. Negative take-off angles are the result of the pelvic girdle of the salamander being above the pectoral girdle at take-off (Fig. 1B). The salamanders with negative take-off angles still left the ground, however, which indicates that these salamanders pushed vertically through the hips to jump, rather than in the direction of the long axis of the body. A linear regression of maximum height vs. take-off angle detected a small positive correlation ( $F_{1,145} = 11.30, P = 0.01, R^2 = 0.07$ ).

DISCUSSION

Salamander jumps are an escape response (Brodie 1977; Ryerson 2013). Tail autotomy is also an escape strategy employed by salamanders, with a subsequent regrowth period of 1–8 mo, depending on temperature, photoperiod,

TABLE 1.—Measures of performance for three species of plethodontid salamanders that jumped across a 5 cm gap before (Y) and after (N) tail loss. Mean values are reported  $\pm 1$  SD, along with the 95% confidence interval (CI).

| Species                         | Maximum height (cm) |                 |           | Take-off angle (degrees) |                   |             | Take-off velocity (m/s) |                 |           |
|---------------------------------|---------------------|-----------------|-----------|--------------------------|-------------------|-------------|-------------------------|-----------------|-----------|
|                                 | Tail status         | Mean $\pm$ SD   | CI        | Tail status              | Mean $\pm$ SD     | CI          | Tail status             | Mean $\pm$ SD   | CI        |
| <i>Desmognathus fuscus</i>      | Y                   | 0.78 $\pm$ 0.27 | 0.67–0.90 | Y                        | 12.58 $\pm$ 6.25  | 9.94–15.22  | Y                       | 0.90 $\pm$ 0.18 | 0.80–0.97 |
| <i>D. fuscus</i>                | N                   | 0.70 $\pm$ 0.20 | 0.62–0.79 | N                        | 8.74 $\pm$ 9.75   | 4.62–12.86  | N                       | 0.91 $\pm$ 0.21 | 0.82–1.00 |
| <i>Desmognathus ochrophaeus</i> | Y                   | 0.74 $\pm$ 0.21 | 0.66–0.83 | Y                        | 13.68 $\pm$ 6.58  | 10.97–16.40 | Y                       | 0.94 $\pm$ 0.24 | 0.85–1.04 |
| <i>D. ochrophaeus</i>           | N                   | 0.68 $\pm$ 0.20 | 0.61–0.77 | N                        | 13.24 $\pm$ 10.28 | 9.00–17.49  | N                       | 0.94 $\pm$ 0.23 | 0.85–1.03 |
| <i>Plethodon cinereus</i>       | Y                   | 0.57 $\pm$ 0.14 | 0.51–0.63 | Y                        | 11.36 $\pm$ 5.22  | 9.10–13.62  | Y                       | 0.86 $\pm$ 0.17 | 0.78–0.93 |
| <i>P. cinereus</i>              | N                   | 0.75 $\pm$ 0.19 | 0.67–0.83 | N                        | 14.63 $\pm$ 10.09 | 10.37–18.89 | N                       | 0.94 $\pm$ 0.26 | 0.82–1.05 |

TABLE 2.—Statistical output of a general linear model analysis for the effects of tail status, species, and their interaction on jumping performance in three species of plethodontid salamanders. Response variables include maximum height, take-off angle, and take-off velocity. Bold-faced values are statistically significant ( $P < 0.05$ ).

| Effect      | Maximum height (cm) |             |         | Take-off angle |             |             | Take-off velocity (m/s) |             |         |
|-------------|---------------------|-------------|---------|----------------|-------------|-------------|-------------------------|-------------|---------|
|             | df                  | F statistic | P value | df             | F statistic | P value     | df                      | F statistic | P value |
| Tail status | 1, 12               | 0.01        | 0.92    | 1, 12          | 0.01        | 0.92        | 1, 12                   | 0.10        | 0.76    |
| Species     | 2, 12               | 0.08        | 0.92    | 2, 12          | 4.66        | <b>0.03</b> | 2, 12                   | 0.46        | 0.64    |
| Interaction | 2, 12               | 2.15        | 0.16    | 2, 12          | 1.54        | 0.25        | 2, 12                   | 0.88        | 0.44    |

and feeding frequency (Marvin and Lewis 2013). Because the tail makes up a significant portion of the body mass and length, we predicted that tail loss would lead to a decrease in take-off performance. Contrary to our predictions, our analysis could not detect a change to take-off angle, take-off velocity, and maximum height attributable to tail loss in three species of plethodontid salamanders. Our analysis detected that *D. fuscus* had a smaller take-off angle than the other salamanders, however, regardless of tail status. Because these salamanders were the largest of the species tested, it is possible that size limited their ability to pick up their torso and head during take-off.

The jump characteristics were highly variable for all subjects with or without tails (Table 1). It appears that salamanders do not need to be consistent jumpers to succeed in their primary task of escape. This seems reasonable because it is advantageous to preserve jump characteristics after tail loss if the salamander wants to retain jumping as an escape response. Although plethodontid salamanders jump with the use of the C-bend jump described by Ryerson (2013) and Ryerson et al. (2016), they are not able to reproduce the same jump consistently (e.g., same take-off angle, take-off velocity). This strategy is acceptable if the task is purely escape; a variable and unpredictable jump may help the salamander elude predators. This jump strategy would not be successful if the purpose of jumping was to land in a specific location, however, such as jumping to a perch; in this case, a precise jump would be advantageous so that the animal lands on the perch without falling off. For example, Gillis et al. (2009) demonstrated that for *Anolis carolinensis* having intact tails, jump take-off angle and take-off velocity measurements had standard deviations of approximately 12% and 5%, respectively, which is much smaller than those in this study (SD for take-off angle and take-off velocity were approximately 67% and 24%, respectively). It seems logical that animals that jump to cover the distance between two nonconnected locations in space are selected to be more consistent in their jump performance. It would be interesting to study jumping consistently for the arboreal plethodontid salamander, *Aneides lugubris*. These salamanders climb trees and thus have larger limbs and tails than our salamanders and also use jumping as an escape response (Ritter and Miller 1899; Ritter 1903; Stebbins and McGinnis 2012). If *A. lugubris* also jumps to move effectively within the arboreal habitat, which is uncertain, we predict that take-off velocity and take-off angle would be more consistent than what we found from our three terrestrial salamander species that use jumping as an escape response.

Across the three species of salamanders, six successful tailless jumps were initiated with negative take-off angles because the subject's pelvic girdle was higher than the pectoral girdle (range:  $-0.8$  to  $-5.9$  degrees; Fig. 2B). At the moment of take-off, the hindlimb was perpendicular to the ground and fully extended, and therefore the pelvic girdle is about a limb length off the ground. The anterior end of the salamander is rotated slightly downwards, leaving the pectoral girdle slightly lower than the pelvic girdle. The salamanders that produced this negative take-off angle also produced positive take-off angles in other jumps. Furthermore, jumps with negative take-off angles produced maximum heights that were close to the group mean, although we did find a positive correlation between angle and maximum height. These data give us some insight into the possible jump mechanism employed by the salamanders. We suggest that the jump mechanism might be the following: the hindlimb that is ipsilateral to the C-bend (on the concave side of the bend) is placed in front of the hips before take-off and thus functions as a strut, lifting the pelvic girdle of the salamander into the air (similar to a pole vaulter's motion). This mechanism would imply that the vertical forces are placed on the pelvis, creating a torque on the center of mass that is placed anterior of the hips. During tail loss, the center of mass is shifted more anteriorly on the salamander's trunk, producing a larger moment arm and thus torque during jump that rotates the torso down.

Our presumed mechanism for the jump provides the question: Why do the tailless jumpers not produce negative take-off angles at higher frequencies, or consistently for a single individual? We suggest that this pattern might have to do with the range of masses and tail sizes for the salamander species included in our analyses. Future research that incorporates species having a greater range of masses might reveal the answer. Further studies should also focus on the kinematics of unsuccessful jumps to obtain an understanding as to why and when salamanders fail to jump, and if this is correlated to take-off angle. For the time being, we can conclude that plethodontid salamanders are still able to jump during tail loss, and do so with relatively similar coordination as compared to tailed salamanders.

The tail could play a role in other parts of the jump, including maintaining in-air stability (pitch/roll/yaw) and landing kinematics, but it is unclear if tail loss alters these traits in salamanders. Tails are important in-air balance organs in several autotomizing lizard families during a jump (Jusufi et al. 2008; Gillis et al. 2009; Libby et al. 2012). Arboreal lizards have developed tail-assisted pitch control mechanisms to help them jump and land with precision as they move from branch to branch (Losos and Irschick 1996; Irschick and Losos 1998). The movement of the lizards' tails leads to angular momentum around the center of mass that shifts the body opposite of the tail (Jusufi et al. 2008). Gillis et al. (2009) found take-off velocity and take-off angle were not changed after tail loss in anole lizards, but in-air stability became inconsistent and led to an atypical landing posture. This indicates that the tail played an active role in manipulating the in-air rotation of the lizard, which might be true for salamanders as well. Qualitatively, salamander in-air and landing postures differed inter- and intraspecifically, and between jumps from the same individual. Our study was limited in this respect, however, because the clarity of our

video recordings was not ideal to measure in-air pitch, roll, and yaw accurately. Salamander landing was not always captured by the camera because the platforms were separated at different heights and salamanders often did not reach the second platform.

Our laboratory trials precluded any conclusions concerning how tail loss affects salamander jump frequency in the field. Little is known about the frequency of jumps used during escape maneuvers in the wild, or if tail autotomy pushes the salamander to prefer other escape strategies such as immobility (Brodie et al. 1974; Brodie 1977; Dodd 1989). A study of salamander defense maneuvers in the field would help us understand the change to salamander escape strategy after tail loss.

**Acknowledgments.**—We thank Allegheny College and the Christine Scott Nelson Fund to A. Hessel for supporting this research. We would also like to thank S. Wissinger for help with locating and collecting salamanders, B. Hersh for providing fruit flies, A. Statman for assistance during this study, and R. St. Laurent for statistical guidance. Anonymous reviewers contributed significant improvements to this manuscript. The Allegheny College Institutional Animal Care and Use Committee approved collection, husbandry, and experimental procedures (2011-001). Salamanders were captured under a Pennsylvania Collection Permit 597 to L. Whitenack.

#### SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at <http://dx.doi.org/10.1655/Herpetologica-D-15-00067.S1>

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Accepted on 28 February 2017  
Associate Editor: Eric McElroy