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Throw your body into it:

Jumping in the salamander *Desmognathus ocoee*

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Short title: Jumping in *D. ocoee*

21 **<u>Summary</u>**

22   Here I describe the kinematics of jumping as seen in the plethodontid salamander,

23 *Desmognathus ocoee*. Using high-speed video imaging techniques, the kinematics and

24 scaling properties of this behavior are quantified. Unlike most terrestrial vertebrates,

25 which use force generated from the hind limbs to jump, salamanders jump by laterally

26 bending and then rapidly straightening the body, using momentum to carry the individual

27 through the air. This movement is strikingly similar to both the terrestrial escape response

28 of mudskippers and terrestrial blennies, and shares a general pattern of movement with

29 the C-start escape response in several aquatic vertebrates. While the axial musculature

30 appears to be responsible for this behavior, it remains to be seen what role the limbs and

31 tail play. Across a two-fold range in body sizes, only duration of bending was correlated

32 with size. The lack of strong scaling relationships suggests a spring mechanism that

33 allows performance to be maintained despite an increase in size.

34

35 **<u>Introduction</u>**

36   Predator-prey interactions represent two opposing sides of natural selection.

37 Predatory behavior that increases the ability to locate and capture prey is favored, while

38 prey behavior that decreases the likelihood of capture is simultaneously favored (Schall

39 and Pianka, 1980). In vertebrates, there are numerous different passive and active

40 mechanisms by which individuals attempt to escape predation(e.g., C-starts in fishes and

41 aquatic amphibians (Azizi and Landberg, 2002; Domenici and Blake, 1997; Hsieh, 2010),

42 camouflage (Alcock, 2009), and jumping in lizards (Toro et al., 2003; 2004)).

43   Plethodontid salamanders, a diverse group of lungless amphibians, possess a

44 myriad of defensive mechanisms to deter predation (Brodie, 1977; Brandon et al., 1979).

45 Individual species exhibit passive mechanisms, including aposematic coloration and

46 toxins secreted through skin (Brandon et al., 1979). These salamanders will also

47 incorporate a range of active mechanisms to avoid predation, including coiling, lashing,

48 writhing or in some cases remaining completely motionless (Brodie, 1977). One species,

49 *Hydromantes platycephalus*, has even been documented rolling itself downhill to escape

50 (Garcia-Paris and Deban, 1995).

51   This study details a previously undescribed mechanism of jumping in the

52 plethodontid salamander, *Desmognathus ocoee*. This mechanism of movement has been

53 mentioned anecdotally as a defensive behavior (Brodie, 1977; Cochran, 1911; Murphy,

54 1917; O'Reilly et al., 2000), but the mechanics of the movement have yet to be described.

55 In this study high speed imaging was used to describe the mechanism by which the

56 salamanders are able to propel themselves through the air. It is hypothesized that the

57 hind limbs are responsible for providing a pushing-off point, but that the axial muscles

58 are the primary force in jumping, as plethodontid salamanders lack the large limbs

59 common in other taxa whose jumping performance has been measured (e.g. fleas

60 (Bennet-Clark and Lucey, 1967) , frogs (Marsh, 1994), kangaroos (Alexander and

61 Vernon, 1973)).

62

63 **Materials and Methods**

64   Twenty individuals of *D. ocoee* representing an ontogenetic series (snout-vent

65 length [SVL] 2.4-5.2 cm) were collected from Highlands, NC, USA, and imaged

66 overhead at 1000 frames/sec using a Photron FastCam high speed camera system

67   (Photron USA Inc., San Diego, CA USA). Image analysis of each jump was conducted

68   using MaxTraq software (Innovision Systems Inc., Columbiaville, MI USA) for

69   kinematics. Salamanders were marked with three white paper discs, placed on the dorsal

70   surface approximating the pectoral girdle, pelvic girdle, and one point halfway between

71   the two girdles (Fig. 1). No glue was required, the moist skin of the salamanders adhered

72   the discs to the skin. Individuals were encouraged to jump five times over a 3 cm gap by

73   tapping metal forceps directly behind the individual, to simulate an approaching predator.

74   Averaged jump values were used for analysis. Seven variables were analyzed for

75   kinematics and scaling relationships: (1) direction of body bend, (2) angle of bending, (3)

76   duration of loading (time to bend), (4) duration of unloading (release of bend during

77   initial stages of jump), (5) duration of jump, (6) velocity of bending, and (7) velocity of

78   unbending. For scaling relationships, angle of bending, durations and velocities were

79   regressed against SVL using SigmaPlot software (Systat Software, USA). Slopes were

80   compared to zero to determine scaling relationship.

81

82   **Results**

83   The salamander *Desmognathus ocoee* utilizes body bending to propel jumping by

84   laterally bending their body along one side, moving the anterior portion of the body

85   towards the tail, and then rapidly straightening the torso (Fig. 2). This rapid movement

86   propels the salamander into the air for total jump duration, from bending to completion,

87   lasting less than 500 milliseconds (Table 1). There was no preference for a bend direction

88   among individuals ($n = 20$, $t = 0.267$, $p = 0.79$). Analysis of the scaling of the kinematic

89   variables found only the relationship between size and duration of loading (slope $\pm$ 95%

90   confidence interval, 0.037 ± 0.031) to be significant. Across the size range measured

91   unload duration was lower than load duration ($n = 20$, $t = 7.35$, $p < 0.001$), and unload

92   velocity was higher than load velocity ($n = 20$, $t = 7.65$, $p < 0.001$, Table 2).

93

94   **<u>Discussion</u>**

95   Jumping as a mechanism for locomotion and escape has evolved independently in

96   invertebrates (e.g., fleas (Bennet-Clark and Lucey, 1967)) and vertebrates (kangaroos,

97   anoles) and the common trend is enlargement of the hind limbs, which generate the

98   necessary force to jump. Here I document the unusual ability of the salamander

99   *Desmognathus ocoee* to jump without the use of enlarged hind limbs. The plethodontid

100 salamander *D. ocoee* relies on axial bending to perform a jump, and become airborne.

101 Jumping is accomplished by bending of the body into a U-shape, followed by rapid

102 straightening of the body. This provides the momentum necessary for the salamander to

103 leave the ground and subsequently travel an indeterminate distance in the air, all within

104 the span of less than a second. The role of axial musculature in salamander locomotion is

105 well documented, primarily its use in walking and swimming (Azizi and Horton, 2004;

106 Bennett et al., 2001; Frolich and Biewener, 1992; O'Reilly et al., 2000). Given the

107 layering of salamander axial musculature and the differing fiber angles of each layer

108 (Schilling and Deban, 2010) it remains to be seen which axial muscles are driving the

109 jumping.

110   Salamander jumping exhibits similarities to the C-start escape mechanism of

111 aquatic vertebrates. The C-start is a rapid escape reflex, originally described in fish,

112 resulting from the stimulus of one Mauthner neuron (Eaton et al., 1977). An action

113   potential originating in the Mauthner cell results in contraction of the contralateral

114   musculature. Rapid lateral bending of the body in fishes increases velocity of initial

115   movements and the likelihood of escape (Domenici and Blake, 1997). Similarly to the C-

116   start response, the head of the individual is bent towards the tail, while the pelvic girdle

117   serves as the anchor point for this behavior (Hsieh, 2010). Amphibious fish, such as the

118   mudskipper (*Periophthalmus argentilineatus*), also rely on axial musculature to escape

119   predation in the terrestrial environment (Swanson and Gibb, 2004). Mudskippers, lacking

120   hindlimbs, generate thrust with their caudal fin, pushing both laterally and downward

121   (Swanson and Gibb, 2004). Blennies in the genus *Alticus*, show similar patterns of

122   movement, but have refined this generalized pattern even further in response to an almost

123   entirely terrestrial existence (Hsieh, 2010). The C-start has also been observed as an

124   escape mechanism in the aquatic larval stage of the plethodontid, *Eurycea bislineata*

125   (Azizi and Landberg, 2002), to escape larger predators. Unlike C-starts in fishes, it is still

126   unknown if these movements in the larval stage are triggered by Mauthner neurons, as

127   they are in fish. It is possible then that the adults are utilizing a true C-start to perform

128   this jumping behavior. The presence of Mauthner cells have been confirmed in some

129   larval plethodontids, but their function in presence in adults have yet to be confirmed

130   (Will, 1991).

131   Scaling properties of jumping revealed only bend duration correlated with size.

132   Larger salamanders performed at similar levels in other variables despite the longer

133   duration of loading. Contralateral activation of the axial muscles while the salamander

134   was bent would allow for maximum tension prior to the jump. Multiple layered axial

135   muscles activated at different times during jumping may result in the rapid straightening

136   of the salamander. This would allow larger salamanders to generate sufficient force to

137   propel their bodies through the air, effectively acting as a spring mechanism.

138   Investigation of the scaling patterns of salamanders has provided examples of a lack of

139   ontogenetic changes in kinematics (Deban and O'Reilly, 2005; Reilly, 1995). *D. ocoee*

140   only change two-fold in size through ontogeny, further testing of this hypothesis would

141   require a species with a greater size range (e.g., *D. quadramaculatus*).

142   Further investigation is needed to elucidate the role of the limbs and tail during

143   this behavior, as well how other species of differing body proportions perform.

144   Plethodontidae is a large and diverse family of salamanders with a multitude of body

145   types and behaviors. It remains to be seen how many members of this family can jump in

146   this manner, and how performance may vary across the family.

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148   <u>**Acknowledgements**</u>

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155   <u>**References**</u>

156

157   1. **Alcock, J.** (2009). Animal Behavior: An Evolutionary Approach, Ninth Edition.

158   Sinauer Associates, Sunderland, CT, USA.

159

160   2. **Azizi, E. and Horton, J.M.** (2004). Patterns of axial and appendicular

161   movements during aquatic walking in the salamander *Siren lacertina*. *Zoology.*

162   **107,** 111-120.

163

164   3. **Azizi, E. and Landberg, T.** (2002). Effects of metamorphosis on the aquatic

165   escape response of the two-lined salamander (*Eurycea bislineata*). *J. Exp. Biol,.*

166   **205,** 841-849.

167

168   4. **Bennett, W.O., Simons, R.S. and Brainerd, E.L.** (2001). Twisting and bending:

169   the functional role of salamander hypaxial musculature during locomotion. *J. Exp.*

170   *Biol.* **204,** 1979-1989.

171
172   5. **Bennet-Clark, H. C. and Lucey, E. C. A.** (1967). The jump of the flea: a study

173   of the energetics and a model of the mechanism. *J. Exp. Biol.* **47**,59 -76.

174

175   6. **Brandon, R.A., Labanick, G.M. and Huheey, J.E.** (1979). Relative palatability,

176   defensive behavior, and mimetic relationships of red salamanders (*Pseudotriton*

177   *ruber*), mud salamanders (*Pseudotriton montanus*), and red efts (*Notophthalmus*

178   *viridescens*). *Herpetologica* **35,** 289-303.

179

180   7. **Brodie, E.D.J.** (1977). Salamander antipredator postures. *Copeia* **1977,** 523-535.

181

182   8. **Carrier, D.R.** (1993). Action of the hypaxial muscles during walking and

183   swimming in the salamander *Dicamptodon ensatus*. *J. Exp. Biol.* **180,** 75-83.

184

185   9. **Cochran, M.E.** (1911). The biology of the red-backed salamander (*Plethodon*

186   *cinereus erythronotus* Green). *Biol. Bull.* **20,** 332-349.

187

188   10. **Deban, S.M. and O'Reilly, J.C.** (2005). The ontogeny of feeding kinematics in a

189   giant salamander *Cryptobranchus alleganiensis*: does current function or

190   phylogenetic relatedness predict the scaling patterns of movement? *Zoology* **108,**

191   155-167.

192

193   11. **Deban, S.M. and Schilling, N.** (2009). Activity of trunk muscles during aquatic

194   and terrestrial locomotion in *Ambystoma maculatum*. *J. Exp.Biol.* **212,** 2949-2959.

195

196   12. **Domenici, P. and Blake, R.** (1997). The kinematics and performance of fish fast-

197   start swimming. *J. Exp. Biol.* **200,** 1165-1178.

198
199   13. **Eaton, R.C., Bombardieri, R.A., and Meyer, D.L.** (1977). The Mauthner-

200   initiated startle response in teleost fish. *J. Exp. Biol.* **66,** 65-81.

201

202   14. **Frolich, L.M. and Biewener, A.A.** (1992). Kinematic and electromyographic

203   analysis of the functional role of the body axis during terrestrial and aquatic

204   locomotion in the salamander *Ambystoma tigrinum*. *J. Exp. Biol.* **162,** 107-130.

205

206   15. **Gans, C. and Parsons, T.S.** (1966). On the origin of the jumping mechanism in

207   frogs. *Evolution.* **20,** 92-99.

208

209   16. **Garcia-Paris, M. and Deban, S.M.** (1995). A novel antipredator mechanism in

210   salamanders: rolling escape in *Hydromantes platycephalus*. *J. Herp.* **29,** 149-151.

211
212   17. **Hsieh, S.-TT.** (2010) A locomotor innovation enables water-land transition in a

213   marine fish. *PLoS ONE* **5(6),** e11197. doi:10.1371/journal.pone.0011197

214

215   18. **Kolbe, J. J. and Losos, J. B.** (2005). Hind-limb length plasticity in *Anolis*

216   *carolinensis*. *J. Herp.* **39,** 674-678.

217
218   19. **Marsh, R. L.** (1994). Jumping ability of anurans. In *Comparative Vertebrate*

219   *Exercise Physiology* (ed. J. H. Jones), pp. 51-111. San Diego: Academic Press.

220

221   20. **Murphy, R.C.** (1917). The jumping ability of *Plethodon* and its possible bearing

222   upon the origin of saltation in the ancestors of the Anura. *Copeia* **1917,** 105-106.

223

224   21. **O'Reilly, J.C., Summers, A.P. and Ritter, D.A.** (2000). The evolution of the

225   functional role of trunk muscles during locomotion in adult amphibians. *Am. Zool.*

226   **40,** 123-135.

227

228   22. **Reilly, S.M.** (1995). The ontogeny of aquatic feeding behavior in *Salamandra*

229   *salamandra*: stereotypy and isometry in feeding kinematics. *J. Exp. Biol.* **198,**

230   701-708.

231

232   23. **Schilling, N. and Deban, S.M.** (2010). Fiber-type distribution of the perivertebral

233   musculature in *Ambystoma*. *J. Morph.***271,** 200-214.

234
235   24. **Schall, J.J. and Pianka, E.R.** (1980). Evolution of escape behavior diversity.

236   *Am. Nat.* **115 (4),** 551-566.

237
238   25. **Swanson, B.O. and Gibb, A.C.** (2004). Kinematics of aquatic and terrestrial

239   escape responses in mudskippers. *J. Exp. Biol.* **207,** 4037-4044.

240

241   26. **Toro, E., Herrel, A., Vanhooydonck, B. and Irschick, D.J.** (2003). A

242   biomechanical analysis of intra- and interspecific scaling of jumping and

243   morphology in Caribbean *Anolis* lizards. *J. Exp. Biol.* **206,** 2641-2652.

244

245   27. **Toro, E., Herrel, A. and Irschick, D.** (2004). The evolution of jumping

246   performance in Caribbean *Anolis* lizards: solutions to biomechanical trade-offs.

247   *Am. Nat.* **163,** 844-856.

248
249   28. **Will, U.** (1991). Amphibian Mauthner cells. *Brain Behav. Evol.* **37,** 317-332.

250

251   **<u>Figure Legends</u>**

252   **Fig. 1:** Individual *D. ocoee* with landmarks for digital analysis with scale. Point 1

253   indicates the pectoral girdle, point 3 is the pelvic girdle, and point 2 is equidistant

254   between the two girdles.

255

256   **Fig. 2:** Representative image sequence of jumping in the salamander *D. ocoee*. Frame

257   numbers are relative to first image, imaged at 1000 fps.

258

259   **Table 1:** Means and standard deviations of the kinematic variables used to describe

260   jumping in the salamander *D. ocoee*. Load duration is the time that the

261   salamander bends its body prior to jumping, and unload duration is the time

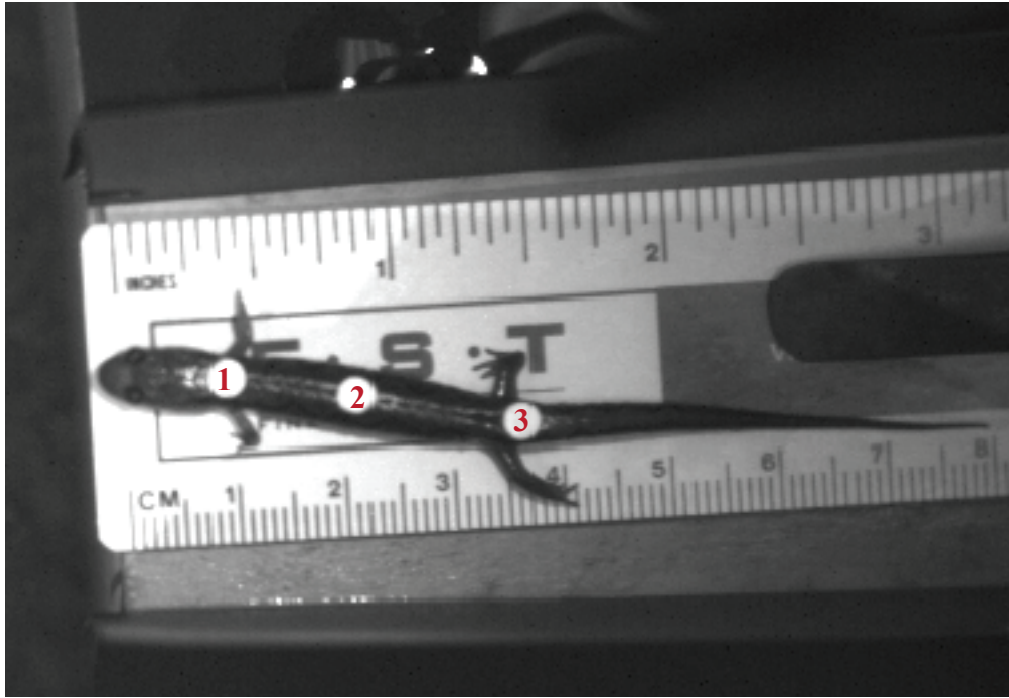262   during which the salamander straightens its body.

Fig. 1: Individual *Desmognathus 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 previous landmarks.
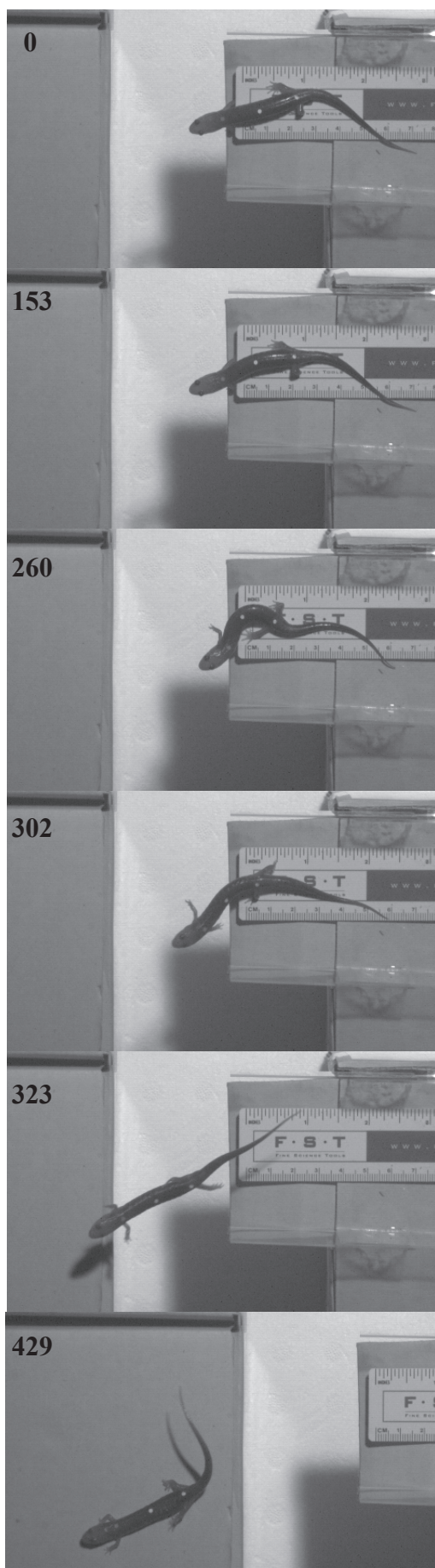
Fig. 2: Representative image sequence of jumping in the salamander *Desmognathus ocoee*. Frame numbers are relative to first image, imaged at 1000 fps.

Variable	N	Mean	Std Dev
SVL (cm)	20	3.3	0.87
Load Duration (s)	20	0.13	0.06
Unload Duration (s)	20	0.04	0.01
Jump Duration (s)	20	0.07	0.02
Bend Angle (deg)	20	41.85	13.85
Load Velocity (deg/s)	20	432.06	277.87
Unload Velocity (deg/s)	20	1216.74	591.8

Table 1: Means and standard deviations of the kinematic variables used to describe jumping in the salamander Desmognathus ocoee. Load duration is the time that the salamander bends its body prior to jumping, and unload duration is the time during the which the salamander straightens its body.