Predatory luring is a behavior that one organism employs (the predator) to attract another organism (the prey) that is presumed consumable to the predator. Some organisms present a lure that resembles prey. If the predatory luring is successful, the potential prey perceive the stimulus as a food item and approach the predator more closely than they might without the stimulus (Reiserer 2002, Hanksncht 2008). Examples of these predatory lures include lingual luring by the mangrove saltmarsh snake (Nerodia clarkia compressicauda; Hanksncht 2008), the dorsal fin of anglerfishes (Pietsch and Grobecker 1978), the tongue of Alligator Snapping Turtles (Macrolemys temminckii; Drummond and Gordon 1979), and the toes of some anurans (Radcliffe et al. 1986, Hagman and Shine 2008). All of the systems in which lures are used and the predator benefits (by ultimately consuming prey that were enticed by a ‘mimic’) have been termed aggressive mimicry (Vane-Wright 1976). Caudal luring, a type of aggressive mimicry, as documented in snakes (Farrell et al. 2011) can be characterized by two distinct qualities: 1) the tail tip is moved in a manner that resembles potential prey and 2) the tail tip is a contrasting color from the body of the predator.

Organisms of the order Odonata (dragonflies and damselflies) are highly predatory insects that are found throughout the world. Substantial data exist on the predatory nature of adult dragonflies, as well as the behavioral modifications of odonate larvae when in the presence of potential predators or other nonpredatory odonates (McPeek 1998, Schaffner and Anholt 1998, Corbet 1999, Stoks et al. 2003, McGruffin et al. 2006, Strobbe et al. 2011). However, there are no reports of larval odonates using predatory luring to entice potential prey within striking distance. Here, we describe predatory luring by both dragonfly (Aeshna palmeta) and damselfly (Argia vivida) larvae. This report involves organisms not previously known to lure prey.

### Materials and Methods

Larvae were collected opportunistically from Tammany Creek, Nez Perce Co., ID (46° 21.51.51 N, 117° 03.32.05 W), a perennial, undammed creek approximately 1–3 m in width and roughly 2 km in length. Tammany Creek drains into the Snake River approximately 770 km from the confluence of the Snake and Columbia rivers.

We surveyed the study area (~1 km in length) on foot and collected odonates by drag net from 15 February 2012 to 12 March 2012. Upon collection, larvae were transported to Lewis-Clark State College and housed in 50-ml plastic vials with a 3-mm-diameter dowel for perching. Larvae were measured with a millimeter rule for total body length and head width and maintained on a photoperiod of 14:10 (L:D) h cycle at an ambient air temperature of 22°C. The range of sizes of Ar. vivida and A. palmeta at this locality during time of collection were Ar. vivida head 2–4.5 mm, body 6–19 mm; A. palmeta head 4–8 mm, body 23–35 mm. Ar. vivida were fed one shrimp (order Mysidae) three times per week. A. palmeta were fed two shrimp 3 times/week. Water was changed after each feeding. Filtered water was used for all housing and experiments.

Behavior trials were conducted in 250-ml containers with filtered tap water and a singular 3-mm-diameter perch. Water was changed and containers were cleaned before each trial. One shrimp was placed in the container, as alternative prey, 1 min after simultaneously placing both odonates in the container. Trials were conducted for 7 min and all behaviors recorded. The ranges of sizes of Ar. vivida and A. palmeta used in behavior trials were Ar. vivida head 3–4 mm, body 11–17 mm; A. palmeta head 4–8 mm, body 23–35 mm.

To evaluate whether the observed behaviors were species specific, we tested A. palmeta and Ar. vivida and conspecifics. Eighteen A. palmeta versus Ar. vivida trials were conducted with randomly chosen animals. Animals used in congeneric trials (not diagrammed) were matched for total body length as closely as possible (31 Ar. vivida vs Ar. vivida and 12 A. palmeta versus A. palmeta).

### Results

In five trials of A. palmeta versus Ar. vivida, a previously undescribed luring behavior was observed by either A. palmeta or Ar. vivida but never both in the same trial. In all trials that luring behavior was demonstrated, the A. palmeta attempted, unsuccessfully, to capture the shrimp prior to the luring behavior. Luring behavior was initiated only when the odonates had entered into the field of view of one another. Once the A. palmeta and Ar. vivida had oriented toward each other, a brief period (~30–60 s) of no visible movement ensued. In four of five trials A. palmeta lured Ar. vivida. The following sequence of events was observed in each trial (Fig. 1).

1. Abdominal movement to the side and exposure of the abdomen of A. palmeta to Ar. vivida. Duration of this movement ranged from 2 to 3 s (Fig. 1A).
2. Ar. vivida changed position to place the abdomen of A. palmeta directly in the field of view (Fig. 1B).
3. Rapid lateral movement of the abdomen of A. palmeta toward Ar. vivida. This behavior consisted of 7–10 movements of the abdomen within approximately 2 s (Fig. 1C).
4. *Ar. vivida* changed orientation toward the luring abdomen (Fig. 1D).
5. *palmata* struck at the head of *Ar. vivida* and began consumption of *Ar. vivida*.

One instance of *Ar. vivida* luring *A. palmata* was observed. The following sequence of events details that observation (Fig. 2).

1. Initial abdominal movement to the side and exposure of the abdomen of *Ar. vivida* to *A. palmata*. Duration of this movement was approximately 8 s (Fig. 2A).
2. The abdomen was then fully moved to the opposite side of the body in a slow motion (~2 s) and held on the other side of the body for approximately 8 s (Fig. 2B).
3. *palmata* changed orientation from the head of *Ar. vivida* to the abdomen of the predatory *Ar. vivida* (Fig. 2B).
4. Step 2 was repeated to the initial side of luring. At this point, *Ar. vivida* was slowly moving toward *A. palmata* (Fig. 2C).
5. *Ar. vivida* positioned its abdomen directly behind its head and slowly continued movement toward head of *A. palmata*. *A. palmata* slowly moved toward the abdomen of *Ar. Vivida* (Fig. 2D).
6. *Ar. vivida* attempted to capture *A. palmata* at its head.
7. Upon being struck, *A. palmata* slowly retreated.
8. *Ar. vivida* continued attempts at luring *A. palmata*, with rapid abdominal movements to the initial side for approximately 5 s. While luring, *Ar. vivida* slowly approached the retreating *A. palmata*.
9. The sequence was broken as *A. palmata* used abdominal thrusts to propel itself away and over *Ar. vivida*.

In the other 13 of 18 *A. palmata* versus *Ar. vivida* trials, no instances of luring were observed. In 7 of 18 trials, *A. palmata* actively pursued the shrimp prey item, catching and consuming the prey without attacking the *Ar. vivida*. During these trials, the *Ar. vivida* positioned itself at the bottom of the chamber and remained motionless for the entirety of the trial. Four of 18 trials resulted in both the *A. palmata* and the *Ar. vivida* pursuing the prey. In all of these trials, the *A. palmata* captured and consumed the prey and subsequently struck at *Ar. vivida* following consumption of the prey regardless of the orientation of *Ar. vivida*. One trial resulted in *Ar. vivida* attempting to consume the prey item after the

Discussion

In our trials, luring occurred only when a head-to-head orientation was present. This is the same orientation described in the well-known agonistic behavior of many larval odonates (Corbet 1999). However, in contrast to previously described agonistic behaviors, predatory luring occurred between different odonate families with a different repertoire of movements (Figs. 1 and 2) and typically ended in consumption of the prey. In trials where luring was not displayed, there was no sustained head-to-head orientation. A caudal attack by either species typically resulted in one of two possible scenarios: 1) removal of lamellae of *Ar. vivida* and subsequent retreat and avoidance of further attack by prey and 2) prey being grasped and subsequent retaliatory bites and aggression resulting in injury to the predator (E.M., personal observations). These two scenarios, we believe, are the reasons for the head-to-head orientation that has been demonstrated as critical for the luring to occur. The caudal luring by the predator caused the lured individual to change orientation slightly to ensure that a successful attack was achieved.

The sequence of motions exhibited during the luring behavior was consistent across all trials. The exaggerated slow swaying of the caudal region caused the lured individual to change orientation. The subsequent rapid movements of the caudal region resembled that of the preferred prey in this environment, the freshwater shrimp, which further provoked the lured individual to investigate. The movement of the lured individual from the head-to-head orientation to the more vulnerable position of focusing on the lure provided the predator an opportunity to strike at the prey. We believe that more instances of predatory luring
would have been observed had the time duration of the trials been longer than 7 min.

The one instance of *Ar. vivida* luring *A. palmata* is of interest. All animals used in the trials were naïve, not having been involved in any trials previously. We cannot comment on the experience of the animals in the field before capture; however, all animals were housed individually for 3 weeks before trials were conducted. The luring demonstrated by *Ar. vivida*, even though consumption was not achieved (although a strike at the head of the much larger *A. palmata* did occur), may indicate that this behavior can be used in situations other than predation. It is possibly used to demonstrate aggressiveness to ward off potential predators. Although the behavior demonstrated by *Ar. vivida* is similar to the agonistic behavior of other Coenagrionidaen odonates (Rowe 1992), several differences exist. 1) The behavior is not directed toward a congeneric. 2) The repertoire of movements is not congruent with those previously described. 3) The behavior displayed by *Ar. vivida* to physically lure the larger *A. palmata* close to the *Ar. vivida*’s abdomen so a successful strike can be delivered (Fig. 2). Testing *Ar. vivida* versus *Ar. vivida* with mismatched sizes and *Ar. vivida* versus *A. palmata* with closely matched sizes will help elucidate whether this behavior is predatory or used to ward off potential predators.

The morphology of *Ar. vivida* may play a significant role in the predatory luring exhibited by *A. palmata*. *Ar. vivida* morphology closely resembles that of small *A. palmata*. Although there was no luring of *A. palmata* by other *A. palmata*, similarity of *Ar. vivida* to *A. palmata* may influence the predatory attack of *A. palmata*. The possibility of predation by a congeneric may induce the larger dragonfly to lure the smaller but morphologically similar damselfly to a position in which a fatal attack is much easier and much more likely. The range of sizes of *Ar. vivida* and *A. palmata* at this locale creates the possibility that large larvae are likely to encounter smaller conspecifics.

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References Cited

Corbet, S. P. 1999. Dragonflies: behavior and ecology of Odonata. Cornell University Press, Ithaca, NY.

Drummond, H., and E. R. Gordon. 1979. Luring in the neonate alligator snapping turtle (*Macrolemys temminckii*): description and experimental analysis. Z. Tierpsychol. 50:136–152.

Farrell, T. A., P. G. May, and P. T. Andreidis. 2011. Experimental manipulation of tail color does not affect foraging success in a caudal luring rattlesnake. J. Herpetol. 45: 291–293.

Hagman, M., and R. Shine. 2008. Deceptive digits: the functional significance of toe waving by cannibalistic Cane Toads (*Chalimus marinus*). Anim. Behav. 75: 123–131.

Hanksnecht, K. A. 2008. Linguistic luring by mangrove saltmarsh snakes (*Nerodia clarkia compressicordata*). J. Herpetol. 42: 9–15.

McGuflin, M. A., R. L. Blaker, and M. R. Forbes. 2006. Detection and avoidance of fish predators by adult *Enallagma* damselflies. J. Insect Behav. 19: 77–91.

McPeek, M. A. 1998. The consequence of changing the top predator in a food web: a comparative experimental approach. Ecol. Monogr. 68: 1–23.

Pietsch, T. W., and D. B. Grobecker. 1978. The complete angler: aggressive mimicry in an attenarian anglerfish. Science 201: 369–370.

Radcliffe, C. W., D. Chiszar, K. Estep, J. B. Murphy, and H.M. Smith. 1986. Observations on pedal luring and pedal movements in leptodactylid frogs. J Herpetol 20: 300–306.

Reiserer, R. S. 2002. Stimulus control of caudal luring and other feeding responses: a program for research on visual perception in vipers, pp. 361–383. In G.W. Schuett, M. Hoggren, M.E. Douglas, and H.W. Greene (eds.), Biology of the vipers. Eagle Mountain publishing, Eagle Mountain, UT.

Rowe, R. J. 1992. Ontogeny of agonistic behaviour in the territorial damselfly larva, *Xanthochnemis zealandica* (Zygoptera: Coenagrionidae). J. Zool. 226: 81–93.

Schaffner, A. K., and B. R. Anholt. 1998. Influence of predator presence and prey density on behavior and growth of damselfly larvae (*Ischnura elegans*) (Odonata: Zygoptera). J. Insect Behav. 11: 793–809.

Stoks, R., M.A. McPeek, and J. L. Mitchell. 2003. Evolution of prey behavior in response to changes in predation regime: damselflies in fish and dragonfly lakes. Evolution 57(3): 574–585.

Strobbe, F., M. A. McPeek, and M. D. Block. 2011. Fish predation selects for reduced foraging activity. Behav. Ecol. Sociobiol. 65: 241–247.

Vane-Wright, R. I. 1976. A unified classification of mimetic resemblances. Biol. J. Linn. Soc. 8: 25–56.