

Modulation in the Feeding Prey Capture of the Ant-lion, *Myrmeleon crudelis*

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ABSTRACT

Ant-lions are pit-building larvae (Neuroptera: Myrmeleontidae), which possess relatively large mandibles used for catching and consuming prey. Few studies involving terrestrial arthropod larva have investigated prey capture behavior and kinematics and no study has shown modulation of strike kinematics. We examined feeding kinematics of the ant-lion, *Myrmeleon crudelis*, using high-speed video to investigate whether larvae modulate strike behavior based on prey location relative to the mandible. Based on seven capture events from five *M. crudelis*, the strike took 17.60 ± 2.92 msec and was characterized by near-simultaneous contact of both mandibles with the prey. Modulation of the angular velocity of the mandibles based on prey location was clearly demonstrated. *M. crudelis* larvae attempted to simultaneously contact prey with both mandibles by increasing mean angular velocity of the far mandible (65 ± 21 rad sec⁻¹) compared with the near mandible (35 ± 14 rad sec⁻¹). Furthermore, kinematic results showed a significant difference for mean angular velocity between the two mandibles ($P < 0.005$). Given the lengthy strike duration compared with other fast-striking arthropods, these data suggest that there is a tradeoff between the ability to modulate strike behavior for accurate simultaneous mandible contact and the overall velocity of the strike. The ability to modulate prey capture behavior may increase dietary breadth and capture success rate in these predatory larvae by allowing responsive adjustment to small-scale variations in prey size, presentation, and escape response. *J. Exp. Zool.* 313A, 2011. © 2011 Wiley-Liss, Inc.

J. Exp. Zool.
313A, 2011

How to cite this article: Lambert EP, Motta PJ, Lowry D. 2011. Modulation in the feeding prey capture of the ant-lion, *myrmeleon crudelis*. *J. Exp. Zool.* 313A:[page range].

Mechanistic studies of the feeding anatomy, morphology, and behavior of animals have played a vital role in our understanding of the evolution and diversity of feeding performance (Wainwright et al., '89; Lauder and Reilly, '94; Wainwright, 2002). One important aspect of prey capture performance is the ability, or lack thereof, to modulate feeding behavior and tailor predator movements to variation in prey attributes (Liem, '78; Lauder, '81). Modulation is the ability to change the pattern of neuromuscular and kinematic events as a direct response to feeding conditions, including prey location, prey types, sizes, and consistency (Nyberg, '71; Liem, '78; Lauder, '83; Wainwright and Lauder, '86; Anderson, '93). The ability to modulate prey capture may confer greater dietary breadth, as well as increased feeding performance and fitness (Nemeth, '97; Van Wassenbergh et al., 2006). Vertebrate predators in particular are able to recognize subtle differences in prey behavior and adjust attack kinematics to increase the likelihood of prey capture (Nemeth, '97).

Modulation during feeding has been shown in teleost and elasmobranch fishes, amphibians, and mammals (Liem, '78; Wainwright and Lauder, '86; Anderson, '93; Van Wassenbergh et al., 2006; Lowry et al., 2007; Ross et al., 2007), but has not been studied in terrestrial invertebrate larvae.

Ant-lions are the larval stage of lacewings (Order Neuroptera, Family Myrmeleontidae) with a large abdomen, small thorax, and two large tapered mandibles. Members of the *Myrmeleon* genus

Grant Sponsor: Porter Family Foundation.

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Received 12 April 2011; Revised 21 July 2011; Accepted 24 August 2011

Published online in Wiley Online Library (wileyonlinelibrary.com).

DOI: 10.1002/jez.709

forage by means of constructing pit-traps using the angle of repose and Stoke's law drag force in loose sediment where large particles are discarded and fine particles are conserved through a sifting and sorting process (Lucas, '82). These traps allow ant-lions to capture small arthropod prey (Griffiths, '80a,b; Heinrich and Heinrich, '84; Cohen, '95). Larvae capture the prey using mandibles (Fig. 1A) that are modified (Fig. 1B) for piercing the tough cuticle, delivering venom or digestive secretions, and removing liquefied prey substances (Cohen, '95).

Fast strike velocities have been shown to be advantageous for a variety of vertebrate and invertebrate predators, including anglerfish, barracuda, dragon fly larvae, gar, needlefish, peacock mantis shrimp, pike, praying mantis, seahorse, and trap-jaw ants (Grobecker and Pietsch, '79; Tanaka and Hisada, '80; Corrette, '90; Harper and Blake, '91; Gronenberg, '95; Porter and Motta, 2004; Patek and Caldwell, 2005; Patek et al., 2006; Spagna et al., 2008; Roos et al., 2009). All these predators employ an ambush or sit-and-wait prey capture behavior, a strategy typical of Myrmeleontidae larvae. However, although work has been dedicated to theories of foraging, biology, and habitat preference (Griffiths, '80a; Heinrich and Heinrich, '84; Farji-Brener, 2003; Scharf and Ovidia, 2006), no work has emphasized the feeding kinematics of the jaw apparatus in Myrmeleontidae larvae or analyzed modulation in the strike of any terrestrial arthropod larva.

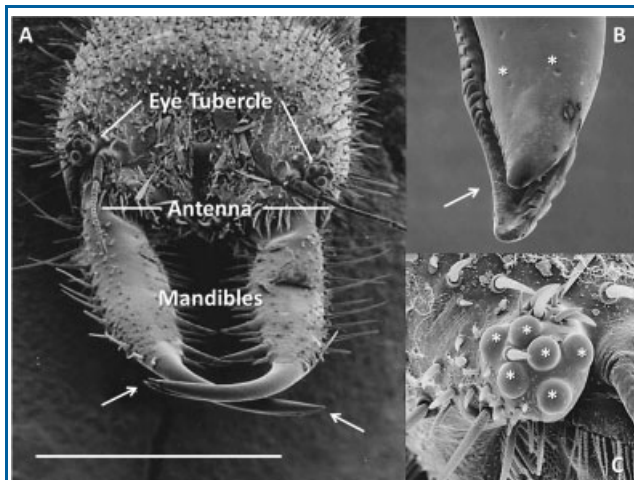


Figure 1. SEM images of *Myrmeleon crudelis* head capsule and mandibles. (A) The external anatomy of the head reveals the location of the eye tubercle containing six stemmata, antenna, and mandibles ($43\times$). Scale bar is 1 mm. Arrows mark slots in the mandibles. The head capsule and the rest of the body are covered with bristles. (B) The distal tip of the left mandible shows the serrated slot (marked with arrows) and sensilla coeloconica (marked by asterisks) ($75\times$). (C) Eye tubercle containing six stemmata ($300\times$). Each stemma is marked by an asterisk. SEM, scanning electron microscope.

Ant-lions have a variety of sensory systems that are specialized to allow them to live in a sandy, subsurface habitat. Campaniform sensilla are mechanoreceptors located on the head, legs, and abdomen that may aid in digging in sandy substrates by detecting stretch forces in the cuticle (Devetak et al., 2010). Chemoreceptors play an important role in the detection of taste and chemical substances. Sensilla coeloconica are chemoreceptors found on the mandibles (Fig. 1B) that aid in detecting diverse chemicals, whereas sensilla basiconica are located on the antennae and aid in olfaction (Devetak et al., 2010). Fertin and Casas (2007) have demonstrated that ant-lions have the ability to sense mechanical waves moving through the sediment allowing the ant-lion to extract directional information. Providing visual information to the ant-lion are its bilateral eye tubercles (Fig. 1A). Each eye tubercle contains six stemmata (Fig. 1C), with each stemma containing 30–70 photoreceptors arranged in a single tier that produce a hexagonally regular netlike rhabdom (Gilbert, '94, Fertin and Casas, 2007).

The *Myrmeleon crudelis* (Walker, 1853) pitfall trap confers considerable benefits with regard to energy expenditure as food is directed to the mandibles of the larva at the vertex of the pit, eliminating the costly pursuit of prey (Mansell, '88). The pitfall trap assists *M. crudelis* larva in sized-based prey selection, provides protection from predators, enables the capture of highly mobile prey, and temporarily disorients prey allowing for rapid prey capture and incapacitation (Griffiths, '80a; Mansell, '88). However, the pitfall trap does present some disadvantages in that the foraging area is limited to the circumference of the trap, location is limited to sheltered areas to avoid thermal stress and, because the energy invested in building and maintaining the trap is high, the larvae are confined to the trap and rarely relocate (Mansell, '88). With the restriction in ant-lion mobility coupled with confinement to the pit there may be evolutionary pressure for developing behaviors that increase prey capture success rate. We postulate that *M. crudelis* larva may have developed the ability to modulate their strike in order to increase prey capture success by maximizing their ability to respond to minor variations in prey type, size, and presentation.

The goals of this study were to: (1) investigate the strike kinematics of larval *M. crudelis* and (2) determine if *M. crudelis* are capable of modulating their strike in response to prey location relative to the mandibles.

MATERIALS AND METHODS

Animals

M. crudelis larvae were collected in April 2009 in sandy sheltered areas in an urban wetland characterized by dry sand, palms, oak trees, and pine trees in Tampa, Florida. Larvae were kept in plastic, 473-mL containers with prepared sediment of washed beach sand. After rinsing with fresh water, the sand was dried for 12 hr in a drying oven at 103.5°C . Dried sand was then sieved

through a 2-mm certified screen to obtain optimal grain size (Farji-Brener, 2003). Larvae were kept on a 12:12-hr light-dark cycle in a 25°C room. Five *M. crudelis* larvae with a mean total length of 9.20 mm (range 8.19–10.30 mm) were recorded via high-speed digital video feeding on the little black ant, *Monomorium minimum*, that were approximately 2 mm in length. Third instar ant-lions were used exclusively and instar stage was determined by mandible length (Lucas and Stange, '81). Third instar stage ant-lions were used due to their larger head capsule and mandible size.

Data Acquisition

To analyze the strike kinematics and test for modulation, *M. minimum* were placed just outside the ant-lion pit-traps with forceps so they could enter the pit-trap naturally, allowing the larval *M. crudelis* to detect prey as they would in nature. Additionally, this presentation method prevented the ant-lion from anticipating prey presence via the detection of any reward predicting stimuli (Schultz, 2004). Prey items dropped directly into the pit-trap, or intentionally placed, are deemed unnatural and unlikely (Heinrich and Heinrich, '84). Upon *M. minimum* entrance into the pit-trap miniature landslides were created sending *M. minimum* toward the vertex of the pit-trap where it could be captured by the mandibles of the larval *M. crudelis*. In prefilming tests, larvae typically ceased feeding after capturing five prey items. During filming tests, individual larvae were never filmed feeding in more than three sequential prey capture events to avoid possible satiation effects. Filming sessions occurred one to two times per week from April 2009 until October 2009.

Video sequences were captured with a high-speed camera (IN500M512, FASTEC Imaging, San Diego, CA) using a macro 35-mm lens at 500 frames per second, with illumination provided by a flood lamp (Lowel Pro-light, 250-W halogen bulb). The experimental traps were maintained at an ambient room temperature of 25°C while filming. The lamp increased (when on) and decreased (when off) ambient temperature at a rate of $\pm 1^\circ\text{C}$ per minute. The experimental traps were never illuminated longer than 1 min and were allowed to cool at least 2 min before the next filming session. The camera was positioned to capture a dorsal view of *M. crudelis* larva. Scale was accounted for by recording a rod of known length (1.951 mm) as close to the *M. crudelis* larva as possible without disturbing the pit or the larva, allowing for length measurements from video sequences. Distance from mandible to *M. minimum* was standardized by scaling the length of the mandibles to 1 mm, calibrating the field of view, thereby removing any possible relationship between mandible size and prey distance to mandible. Distance between the mandible and prey was then measured from the distal tip of the mandible to the nearest part of the *M. minimum* exoskeleton (i.e., nearest point on the body not including the legs or antennae). All distance measurements were measured using Redlake MotionScope PCI version 2.30.0 software.

Video sequences were analyzed frame by frame using ImageJ software version 1.44. Only video sequences in which *M. crudelis* larva successfully captured *M. minimum*, both mandibles remained in the same plane of the camera, and prey was not on or touching the larva's mandible before the feeding event were used for analysis (Fig. 2). Seven capture events were analyzed for each of the five *M. crudelis* larvae. Measurements of striking events were recorded from the frame before first mandible movement until both mandibles contacted the prey. To account for head motion during the strike, a tangential line was constructed running through the eye tubercles. The midpoint between the eye tubercles was measured and digitized as well as the distal tips of the mandibles (mandibles act as a thin rod, which rotates about a fixed axis). A line was constructed connecting the midpoint of the eye tubercles to the tip of the mandible creating an angle (Fig. 2A). The change in angle through time allowed for the calculation of angular velocity of the mandible tips, delay of the onset of motion of the near mandible relative to the far (delay), and the length of the strike event (time to contact).

To examine morphological features of *M. crudelis* larvae, scanning electron micrographs were taken. The unfixed *M. crudelis* larva head was mounted on carbon-impregnated double-sided tape with silver paste (Electron Microscopy Sciences, Hatfield, PA). After the paste dried, the sample was sputter-coated with 30 nm coating of gold-palladium in a Hummer IV sputter coater (Anatech, LTD, Alexandria, VA). The sample was photographed at 10 kV accelerating voltage in a JEOL JSM 35 scanning electron microscope (JOEL USA, INC., Peabody, MA). Photographs were obtained using Polaroid type 55 film.

Statistics

To compare the motion of mandibles during the strike, each mandible was identified as either near or far based on their location relative to the prey. For both mandibles, each of the three variables, angular velocity, delay in onset of motion relative to the initiation of the strike, and time to prey contact were evaluated via two-way analysis of variance (ANOVA) using Systat 13. This examined differences among individuals, between mandibles, and interactions between individuals and mandibles regardless of the distance of the mandible tip to the prey. ANCOVA could not be used to simultaneously determine the presence and extent of covariation in individual and mandible effects with distance from each mandible to the prey (continuous variable) because the sample size was too small to accommodate so many nested effects. Angular velocity and distance to prey data were not transformed before analysis because they met the assumption of normality (Kolmogorov-Smirnov $P = 0.282$ and 0.174 , respectively), but delay in onset and time to contact data were log transformed.

In order to evaluate whether the *difference* in distance between the prey and each mandible (i.e., near vs. far) could

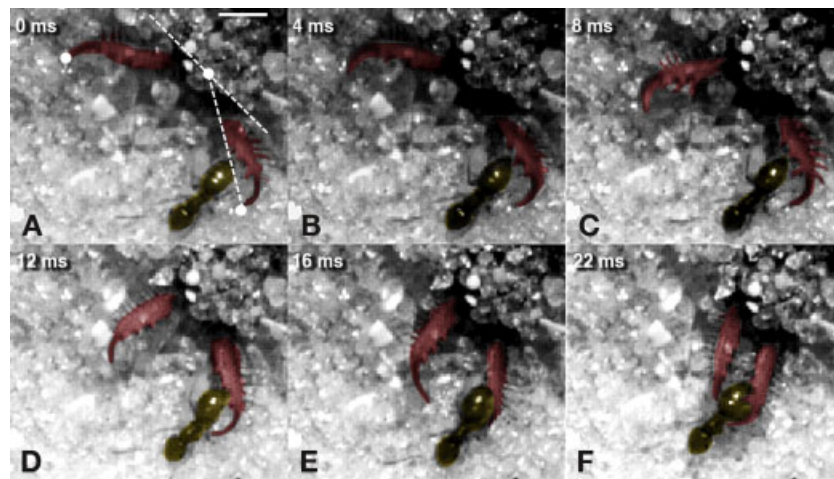


Figure 2. Video frames from a sequence depicting a successful prey capture strike by a *Myrmeleon crudelis* larva on a *Monomorium minimum*. The numbers in the upper left corner represent time and the scale bar is 1 mm. Mandibles are highlighted by the color red and the ant highlighted by the color yellow. The prey is initially located close to the larva's left mandible (near mandible) and remains stationary as the right mandible (far) engages in the strike. The left mandible (near) delays onset of strike before engaging. Frame A depicts landmarks used to reference the motion of the mandibles.

predict the *difference* in angular velocity, delay in onset, and time to prey contact between the near and far mandibles, we conducted three regression analyses. This achieved the same goal as conducting an ANCOVA for each response variable, however because data are pooled, it does not allow for the isolation of individual effects. Pooling of individuals is justified because of low individual variability (Table 1). All values were log transformed and these tests were conducted with the software program R (using the “lme” function in the “nlme” package). When a significant regression coefficient was detected (angular velocity), coefficients were calculated for the near and far mandibles separately for the given variable and compared against one another, as well as against a slope of 1, using a *t*-test in Systat 13. A slope of 1 indicates that mandible angular velocity increases isometrically with distance to the prey, whereas a slope less than this suggests a performance limitation as distance increases.

RESULTS

The mean duration of the prey capture strike was 17.60 ± 2.82 msec. Larval *M. crudelis* exhibited statistically significant differences between the near and far mandibles for angular velocity, delay in onset, and time to prey contact during the strike (Table 1). Individual differences were detected for delay in onset, but not for either of the other variables (Table 1). Interactions between the factors individual and mandible, however, were apparent for both angular velocity and delay in onset (Table 1). Taken together these results indicate that while some variation exists among individual *M. crudelis* larvae, a

common finding in behavioral studies, systematic modulation occurred in the behavior of the mandibles for all variables quantified.

Regression analysis identified a relationship between angular velocity and the difference in distance from the near and far mandibles to the prey ($P = 0.024$, slope = 0.012 ± 0.004 (SE), $F_{1,4} = 12.40$), indicating that *M. crudelis* modulate mandibular speed based on the distance of each to the prey. However, there was no relationship between the difference in delay of the two mandibles to the difference in distance ($P = 0.637$, slope = 0.0649 ± 0.128 (SE), $F_{1,4} = 0.259$) signifying that *M. crudelis* are not modulating the delay of mandible movement in response to variation in the distance from the mandibles to the prey. There was also no relationship between the difference in time to contact of the two mandibles and the difference in distance ($P = 0.637$, slope = 0.0649 ± 0.128 (SE), $F_{1,4} = 0.259$) indicating that *M. crudelis* are not modulating the strikes by differences in time to contact, and near-simultaneous contact was typical. This analysis indicates that larval *M. crudelis* are only capable of modulating their strike with respect to distance by adjusting the angular velocity of their mandibles (Table 2).

When the mandibles were treated separately, angular velocity increased as the distance from the prey to the near (slope = 0.21, $R^2 = 0.12$, $P = 0.040$) and far mandible (slope = 0.65, $R^2 = 0.25$, $P = 0.002$) increased. Slopes of the regressions between the angular velocity of each mandible and the distance to prey were different (Student's $t = 1.93$, d.f. = 66, $P = 0.021$). The slopes of the angular velocity of the near and far mandibles also were significantly less than the isometric slope of 1 (Student's $t = 4.53$,

Table 1. Two-way ANOVA results for strike variables describing relationships between individuals, near and far mandibles, and the interactions between the mandible and the individual.

Variable	Factor	d.f.	F-ratio	<i>P</i>
Angular velocity (rad sec ⁻¹)	Individual	4	1.01	0.412
	Mandible	1	54.30	<0.001
	Individual × Mandible	4	2.53	0.050
Delay in onset (msec)	Individual	4	4.29	0.004
	Mandible	1	51.58	<0.001
	Individual × Mandible	4	4.29	0.004
Time to prey contact (msec)	Individual	4	2.04	0.100
	Mandible	1	17.63	<0.001
	Individual × Mandible	4	1.47	0.220

Significant *P*-values are bold.

Table 2. Regression analysis results for strike variables describing differences between the near and far mandibles for five *Myrmeleon crudelis* larvae (mean ± SD).

Variable	Near	Far	<i>F</i> _{1,4}	<i>P</i> -value
Angular velocity (rad sec ⁻¹)	35.00 ± 14.10	65.40 ± 21.20	12.40	0.024
Delay (msec)	2.74 ± 2.66	0 ± 0	0.26	0.637
Time to prey contact (msec)	14.90 ± 2.88	17.6 ± 2.82	0.26	0.637

Mean values for the near and far mandibles are shown as an average of all 35 strikes. Delay of the near mandible was expressed relative to the start of the far mandible, resulting in zero values for the far mandible. Because Delay values are directly related to Time to prey contact values, their significance values are identical. Significant *P*-values are bold. *N* = 35 mean ± SD.

d.f. = 33, *P* < 0.001 and Student's *t* = 2.00, d.f. = 33, *P* = 0.026, respectively). As the angular velocity of the near mandible increases more slowly than the far mandible with increased distance to the prey, the near and far mandibles of *M. crudelis* larvae move at coordinated, but different, speeds during the strike (Fig. 3). The end result is simultaneous contact of the mandibles with the prey and minimization of the temporal window in which prey can initiate an escape response before complete immobilization.

DISCUSSION

Kinematic analysis of strikes demonstrates that *M. crudelis* larvae have the ability to modulate prey capture behavior, by adjusting the angular velocity of their mandibles based on the relative proximity of each mandible to the prey, in order to achieve simultaneous prey contact. The near and far mandibles behaved independently of one another during the strike and the angular velocity of the mandibles increased with negative allometry as distance increased. Regardless of this, the far mandible angular velocity increased at a higher rate than the near mandible (Fig. 3). Although there was a difference in delay of onset of movement of the two mandibles, the onset of strike behavior was not related to

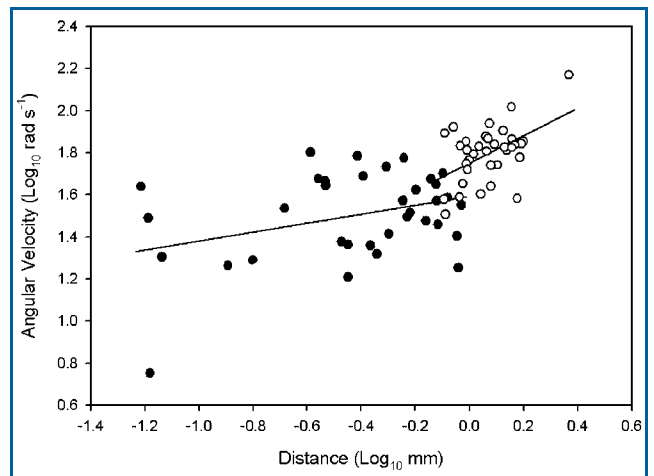


Figure 3. A scatter plot with linear regression plotting the log transformed mean angular velocity of the near (●) and far (○) mandibles of each strike against the initial log transformed distance of the prey to that respective mandible (*N* = 5 individuals with seven strikes each).

the prey's location relative to either mandible, as revealed by the regression analysis. Therefore, delay of the near mandible, in conjunction with modulated angular velocity of both mandibles, resulted in high prey capture efficiency.

Negative allometry of the relationships for the near and far mandibles suggests that as distance of the mandible from the prey increases the relative angular velocity slows. Though this result is intuitive for the near mandible, which slows in order to accommodate simultaneous prey contact of both mandibles, it is an unexpected result for the far mandible, which should speed up. Assuming isometry or slight positive allometry is optimal (Wilkie, '50; Bourke et al., 2008; Wroe et al., 2008), this suggests that the ant-lions tested may strike prey at a less than optimal gape angle with regard to the contractile capability of the muscles involved. It is possible that muscles controlling mandible closure are at a nonoptimal point in the force tension curve resulting in slower velocity of contraction with greater stretch, and suggesting a performance limitation of the feeding apparatus. Negative allometry in the far mandible may also be a result of the small sample size given the low R^2 value (Fig. 3).

The ability of ant-lions to modulate strike kinematics may increase prey capture success rates. By closing the mandibles on the prey at the same time, ant-lions: (1) reduce the chance of elusive prey escaping by minimizing the temporal window for reaction; (2) nullify tactically triggered escape responses in a direction tangential to first predator contact; and (3) reduce or prevent the prey being deflected out of the way by the first mandible if they struck at different times (Motta, '84; Nemeth, '97). Other factors that contribute to successful captures include pit location, pit maintenance, and pit construction (Griffiths, '80a; Heinrich and Heinrich, '84; Farji-Brener, 2003). Ant-lions are capable of catching and consuming a variety of prey types (Heinrich and Heinrich, '84) and such dietary diversity has been correlated with feeding modulation among some teleost fishes (Liem, '78; Nemeth, '97; Van Wassenbergh et al., 2006).

M. crudelis larva strikes reach velocities of 0.244 m sec^{-1} , which is relatively slow when compared with other fast-striking invertebrates (20 m sec^{-1} for peacock mantis shrimp, *Odontodactylus scyllarus*, Patek and Caldwell (2005); 60 m sec^{-1} for trap-jaw ant, *Odontomachus bauri*, Patek et al. (2006)). *M. crudelis* larvae may trade strike velocity for the ability to modulate their strike. As sit-and-wait predators, *M. crudelis* larvae depend on mobile arthropods as their primary food source, resulting in unpredictable prey encounters and decreased volume of prey captured per day (Huey and Pianka, '81). Some mobile invertebrate predators (trap-jaw ant and peacock mantis shrimp) rely on high-velocity strikes and are not known to modulate their strikes (Gronenberg, '95; Patek and Caldwell, 2005; Patek et al., 2006; Spagna et al., 2008). *M. crudelis* larvae use their sensory systems to target the prey's location and have the ability to precisely control their mandibles during the strike allowing for accurate, simultaneous mandible contact with the prey. The

tradeoff between accuracy and speed has been well documented (Reed, '73; MacKay, '82) and we hypothesize that it is this tradeoff that *M. crudelis* larvae exploit, in the context of the pit-trap, to increase prey capture success under conditions where prey are disoriented and incapable of employing typical escape strategies.

Temperature has a crucial role in insect muscle function and ant-lion metabolic rates (Lucas, '85; Stevenson and Josephson, '90; Van Zyl et al., '97). In our experimental environment, *M. crudelis* larvae were observed to cease feeding below 20°C . Cessation of feeding at colder temperatures may be a function of decreased power output of the mandible muscles (Stevenson and Josephson, '90). Because the metabolic rate increases at cooler temperatures in ant-lions (Lucas, '85; Van Zyl et al., '97), ant-lions move subsurface about the pit to control their metabolic rate during the hottest and coldest part of the day, seeking out a desirable temperature (Griffiths, '80a; Lucas, '85). This study examined feeding at temperatures consistent with previous studies investigating feeding kinematics and feeding behavior in terrestrial arthropods (Lucas, '85; Napolitano, '98; Paul and Gronenberg, '99).

Though modulation has been demonstrated here, changes in prey capture behavior over ontogeny and in response to prey type remain unknown. Griffiths ('80a) found that in the third instar ant-lion stage, the majority of metabolic energy is delegated to maintenance and not predation, as is the case with first and second instar larvae. To completely describe ant-lion strike kinematics, it is necessary to study all three instar stages. Further kinematic analysis should test all instar stages for evidence of prey size influencing strike kinematics, common in many vertebrates (Liem, '78; Wainwright and Lauder, '86; Anderson, '93; Van Wassenbergh et al., 2006; Ross et al., 2007), and examine the effect satiation has on feeding performance (Sass and Motta, 2002). An additional avenue of research that has yet to be investigated for Myrmeleotidae larvae is the functional morphology of the mandibles. The slots in the mandibles (Fig. 1B) may be employed to facilitate transport of liquefied prey substances (Prakash et al., 2008), facilitate the restraint of prey by acting as a hook or barb, or have no functional ability and simply be a constructional constraint (Barel et al., '89; Schwenk, '94, '95).

In summary, *M. crudelis* larvae are capable of modulating strike kinematics with respect to the location of their prey. Modulation occurs primarily by means of varying angular velocity of the two mandibles. Modulation of the strike allows both mandibles to contact the prey nearly simultaneously most likely reducing the chances of prey escape.

ACKNOWLEDGMENTS

We thank two anonymous reviewers for their constructive comments as well as L. Habegger, E. Haller, T. Hsieh, K. Mara, and J. Rohr for assistance with the manuscript. Dominic Motta

provided the curiosity that sparked this study. This work was completed through the financial support from the Porter Family Foundation. Equipment was generously provided by a grant to P.J.M. from the University of South Florida Office of Undergraduate Research.

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