RESEARCH ARTICLE

Patterns of variation in feeding strike kinematics of juvenile ghost praying mantis (*Phyllocrania paradoxa*): are components of the strike stereotypic?

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ABSTRACT

Functional systems, such as feeding mechanics, often involve the evolution of several components of the musculoskeletal system that are moved in coordination to capture prey. Because these systems often involve the quick movement of several structures, some feeding systems have been hypothesized to be stereotypic. While the motor activity patterns are often stereotyped, the subsequent kinematics can be variable, many times in response to variation in prey stimulus (e.g. prey position). Patterns of feeding kinematics have been well studied among vertebrates, with less attention on invertebrate systems. The goal of this study was to examine the amount of stereotypy in the feeding strike kinematics of praying mantises. We filmed eight juvenile ghost praying mantises (*Phyllocrania paradoxa*) at 1000 Hz across several days within instar 7. We digitized several points that represent the movement of the coxa, trochanter–femur and tibia of the raptorial foreleg to obtain a set of kinematics including angles and angular velocities of the joint, as well as body lunge. Using the coefficient of variation, we found less stereotypy in the approach stage of the strike compared with the sweep. Using Bonferroni-corrected Pearson's correlations of kinematics with prey position, we found few traits related to prey position with the exception of some kinematics of the coxa joint and the amount of lunge used during the strike. Our results suggest that several components of the praying mantis strike are stereotypic, while others exhibit flexibility to ensure successful capture of the prey.

KEY WORDS: Mantodea, Prey capture, Stereotypy, Feeding mechanics, Coefficient of variation, Motor patterns

INTRODUCTION

Complex functional traits, such as feeding and locomotion, involve the coordinated movements of several components of the musculoskeletal system (Alexander, 2003; Biewener, 2003; Svanbäck et al., 2002; Wainwright et al., 2007). Because of the importance of both of these traits to fitness, the integration of various physiological systems and the speed of movement in many of these systems, it has been debated whether these functional traits are stereotypic (e.g. a reflex); that is, once the behavior is initiated, how much variation exists? Stereotypy can be defined as 'the extent of variation in a behavior under a given set of conditions' (Wainwright et al., 2008), and has been quantified by examining the repeatability of the trait (i.e. the amount of within-individual variation; Boake, 1989; Oufiero and Garland, 2009) and the coefficient of variation (CV; i.e.

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the standard deviation as a percentage of the mean trait value; Rice and Westneat, 2005; Wainwright et al., 2008). If a trait exhibits low variability and/or high repeatability, it is considered a stereotypic response. Conversely, if the trait can be modulated resulting in high variability and low repeatability, then it is not considered stereotypic.

Interpretations of the amount of stereotypy in a functional response are often difficult because of the variation in traits reported and focus of the system. In functional systems, such as feeding and locomotion, the coordinated movements of the parts of the system are often stereotyped in their patterns. That is, key events often occur in the same order. For example, in many fish that utilize suction feeding, the relative timing of events such as maximum gape, hyoid depression and cranial rotation happen in the same pattern because of the nature of the musculoskeletal system (Oufiero et al., 2012; Rice and Westneat, 2005). Similarly, many fish exhibit a C-start escape response, where the body bends into a 'C' to generate thrust and escape the predation threat (Domenici and Blake, 1997). However, while the motor activity patterns may be stereotyped in these systems, the speeds, magnitudes and absolute timing of events may be modulated or exhibit flexibility based on variation in stimuli (Domenici, 2010; Domenici et al., 2011; Jornod and Roche, 2015; Kagaya and Patek, 2016; Oufiero et al., 2012). Therefore, stereotyped behaviors may show consistent motor patterns, but flexibility in kinematics in response to variation in stimuli, such as prey position. For instance, during suction feeding in many fish, a prey item that is farther away may elicit strikes with greater body speed and a larger gape, but when the mouth starts to open in relation to the hyoid depression is relatively consistent (Oufiero et al., 2012). If the resulting kinematics are stereotypic, a predator would have to balance these fixed movements with prey position to successfully capture their target. This may limit the range of positions a predator can strike within to be successful. Conversely, if a predator has the ability to modulate or exhibit flexibility in one part of the integrated system, this may allow for a greater range of attack (Corrette, 1990; Montuelle et al., 2012; Nemeth, 1997). Although many of these relationships have been examined in vertebrate feeding systems, such as suction feeding among fish, there are fewer examples from invertebrate predators (Corrette, 1990; deVries et al., 2012; Kral et al., 2000; Patek et al., 2004).

The goal of the present study was to determine the amount of stereotypy and modulation in the unique feeding mechanisms found among praying mantises. Praying mantises (Mantodea) are a group of more than 2000 species of insects that have evolved exaggerated forelegs, which are used to rapidly capture prey (Lavine et al., 2015; Svenson and Whiting, 2004, 2009); these forelegs constitute a type of raptorial appendage that has evolved independently several times among invertebrates (Corrette, 1990; deVries et al., 2012; Kral et al., 2000; Lavine et al., 2015; Patek et al., 2004). Many praying mantises are ambush predators and rely on camouflage to quickly

capture unsuspecting prey (Svenson and Whiting, 2009). The forelegs of praying mantises comprise three main segments, the coxa, the trochanter–femur and the tibia, which move in a coordinated fashion to capture prey (Copeland and Carlson, 1979; Corrette, 1990; Iwasaki, 1991; Maldonado et al., 1967; Prete and Cleal, 1996; Prete et al., 1990). On the tip of the tibia is a tarsus that is used when walking, but folds back during feeding (Corrette, 1990). Along the inner sides of the femur and tibia are both movable and immovable spines that vary among species in their size, shape and number, which serve to trap the prey in between the tibia and the femur (Loxton and Nicholls, 1979). The strike of the mantis has been broken up into two main components, the approach and the sweep (Fig. 1). The approach (Fig. 1A) serves to position the mantis for the sweep and is typically accompanied by the elevation of the coxa and the extension of the tibia, while the sweep (Fig. 1B) consists of the very rapid extension of the trochanter–femur and the flexion of the tibia simultaneously (Corrette, 1990; Maldonado et al., 1967). Mantises also exhibit a component of lunge in the strike: movement of the remaining legs to get closer to the prey (Copeland and Carlson, 1979).

Several hypotheses have been proposed for the modulation and stereotypy of the mantis feeding strike. Our goal was to use juvenile mantises, which have not been well investigated, to evaluate these hypotheses and determine whether components of the feeding strike are more stereotyped than others, as well as the influence of prey position. First, because the approach sets up the mantis for the sweep by potentially targeting on the prey item, whereas the sweep captures the prey, it has been predicted that the sweep will be more stereotyped compared with the approach (Corrette, 1990). We therefore compare timing of the stages as well as the angles and angular velocity of the joints during both the approach and the sweep. Second, because the flexion of the tibia encloses the prey item in the spines of the femur and tibia, it has been suggested that tibia flexion will be more stereotyped than other components of the foreleg (Corrette, 1990). We therefore look at the variation in flexion velocity compared with the variation in velocities of the other joints. Third, it has been proposed that mantises will exhibit faster strikes with greater prey distances to ensure the prey item is reached before it has time to escape (Lavine et al., 2015; Maldonado et al., 1967). However, which of the components (e.g. approach, sweep, velocity of foreleg segments, etc.) of the feeding strike that will be modulated to increase speed based on prey distance has not been examined in detail. Last, we examine whether the approach sets up the predator to be in position to strike or whether strikes are modulated during the sweep, by examining the relationship between prey position and the angles of the joints at the end of the approach and maximum angles (Corrette, 1990). In addition to these specific hypotheses, we also explore other relationships to determine which components of the feeding strike may be modulated based on prey position, such as the amount of lunge used during the strike, which has been suggested as not being stereotypic (Prete and Cleal, 1996), compared with the amount of foreleg used to capture the prey.

MATERIALS AND METHODS
Eight ghost praying mantises [Mantodea, Hymenopodidae, *Phyllocrania paradoxa* (Burmeister 1838)] were obtained from the hobby industry as juveniles (instar 4). Mantises were housed individually in 2.5 gallon (9.46 litre) aquaria with plastic lids, paper towel substrate and a wooden dowel in the center of the tank spanning the length of the long axis of the tank for perching and filming (Fig. 1, Movies 1, 2). Mantises were fed termites (*Reticulitermes flavipes*) and crickets (*Acheta domestica*) throughout

development until they reached instar 7, the last juvenile stage. Although these mantises may feed primarily on flying prey in nature, the termites and crickets allowed us to film and feed them on consistent food items. Cages were misted several times a week to provide drinking water, the lights in the room were on a 12 h:12 h light:dark cycle and room temperature was maintained at ~23°C.

To obtain feeding strikes, mantises were filmed feeding only on termites in the cages in which they were housed in order to minimize stress. We fed them several termites every 3–4 days (with no feeding in between to ensure motivated strikes) to obtain at least four successful feeding strikes useful for analyses (lateral view and in focus) during each feeding trial. Each mantis, in its cage, was positioned in front of a high-speed camera (Fastec IL3-100S, Fastec Imaging, San Diego, CA, USA). If the mantis moved along the perch, the entire cage was moved to minimize stress to the animals. However, we found that the mantises did not mind being handled or positioned, and they fed with forceful strikes if they were moved by hand. We filmed feeding strikes at 1000 Hz, with a shutter speed of 50 µs to minimize blur between the frames. Each mantis was illuminated with a Nila Zaila LED light (Nila, Altadena, CA, USA), which provides enough illumination at high filming speeds without the added heat of halogen lights. Termites were introduced by tethering them to a piece of fishing line. The termite was then placed in front of the mantis and moved side to side and front to back in a random manner, until the mantis targeted on the prey and struck (Movies 1, 2). After a prey item was captured, we let the mantis eat and process the termite and the sequence was repeated until the mantis was satiated or four successful strikes were recorded each day. We filmed feeding events across several days (e.g. 3–4 days) within the instar to capture any among-day variation in feeding strikes, with each feeding day separated by 3–7 days. Therefore, several mantises were filmed on four separate days, resulting in a total of eight strikes analyzed, and some were filmed on three separate days, resulting in six strikes analyzed (Table 1). One of our individuals would not feed consistently in a position for filming, resulting in fewer videos for this individual (*P. paradoxa* 6; see Table 1). We retain it in the analyses, as we are more interested in overall variation in strikes. A total of 58 videos from the eight mantises were obtained for analysis (Table 1), and include the two fastest strikes based on the flexion velocity of the tibia for each day of filming (see below).

We digitized seven total points on the praying mantis body, the closest foreleg to the camera and the prey, using the MTrackJ plugin for ImageJ (http://imagej.nih.gov/ij). The points are shown in Fig. 1C (see also Movie 1), with point 1 being the attachment of the coxa to the prothorax, point 2 the trochanter–femur joint, point 3 the femur–tibia joint, point 4 the tip of the tibia, point 5 the tip of the tarsus (not used in further analyses), point 6 the attachment of the middle coxa to the mesothorax, and point 7 the position of the prey.

Kinematics
From six of these seven points we obtained kinematics similar to a previous study of mantis feeding strikes (Corrette, 1990). Prey distance was obtained as the linear distance of point 7 from point 1; this differs slightly from another study that obtained the distance of the prey from the mantis's eye (Prete et al., 1990), but is similar to a previous kinematic study of mantis feeding (Corrette, 1990). Prey angle was obtained as the angle at point 1 in between the segments of the body (point 1 to point 6) and predator–prey distance (point 1 to point 7). Time to prey capture was obtained as an estimate based on when the prey (point 7) crosses into a polygon formed by points 2 (trochanter/femur), 3 (tibia/femur) and 4 (tip of tibia), which
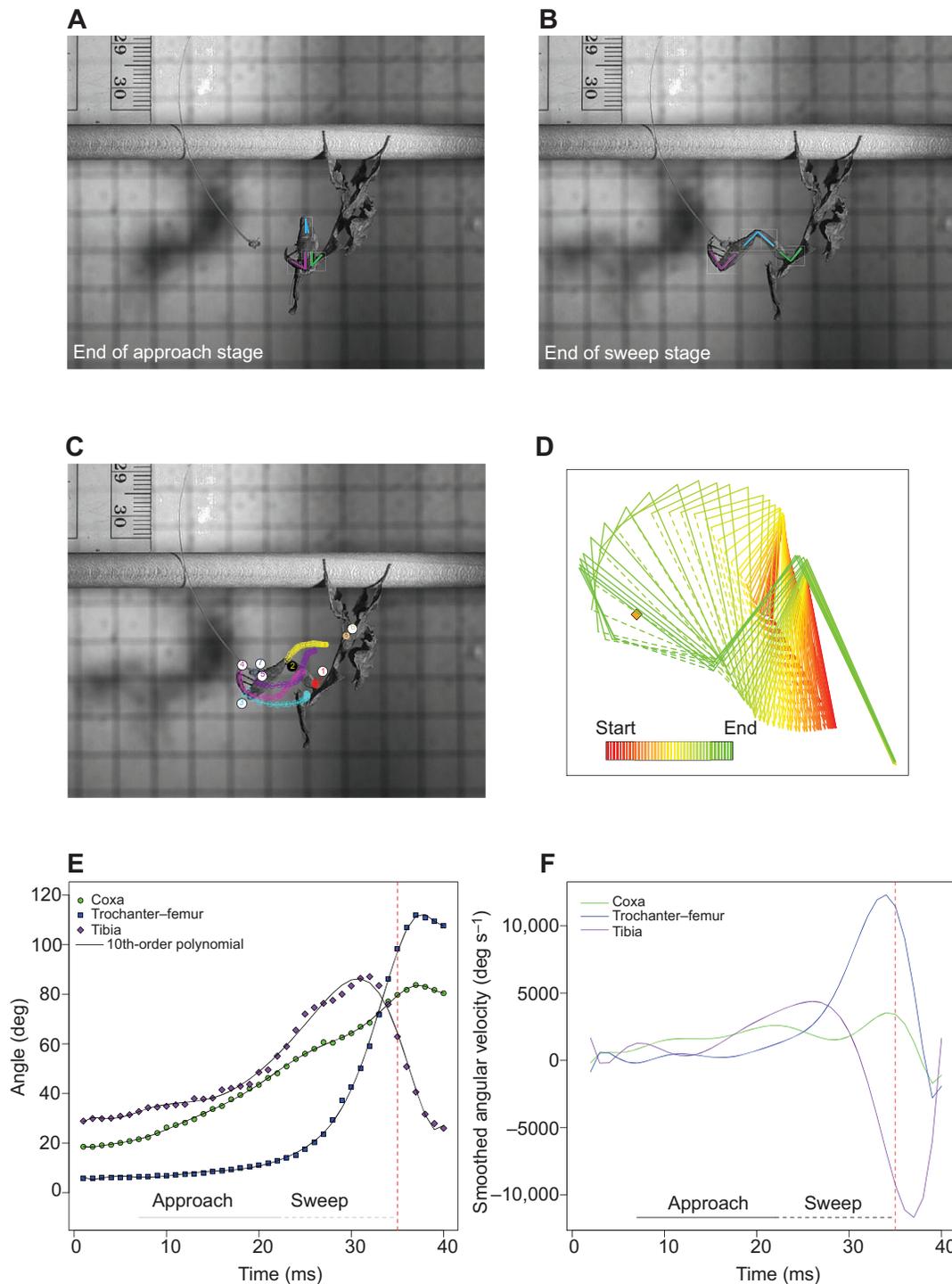
Fig. 1. A representative feeding strike of a juvenile ghost praying mantis (*Phyllocrania paradoxa*). The companion videos can be found in the supplementary material (Movies 1, 2) for this particular strike (Movie 1). (A) The end of the approach stage with extension of the coxa (green) and tibia (purple); the femur (blue) does not move much during this stage. Colored angles are for demonstration and do not represent real digitized points. (B) The end of the sweep when the prey is captured as it crosses into a 'prey-capture zone', as identified as an imaginary line between the tip of the tibia and the trochanter–femur. The sweep stage is represented by further extension of the coxa, rapid extension of the femur and extension followed by rapid flexion of the tibia. (C) The points used to obtain kinematics, followed throughout the strike depicted in A and B. Point 1 is red and represents the coxa–prothorax joint; point 2 is yellow and represents the trochanter–femur joint; point 3 is light blue and represents the tibia–femur joint; point 4 is light purple and represents the tip of the tibia; point 5 is dark purple and represents the tip of the tarsus (not used in analyses); point 6 is beige and represents the leg–mesothorax joint; and point 7 is dark blue and represents the prey. (D) Using the digitized points in C, a computer model of the mantis can be generated. The solid lines are actual body segments; the dashed lines are the hypothetical lines encasing the prey-capture zone. This graph illustrates the movement of the mantis throughout the strike with red representing the beginning of the strike and green representing the end of the strike. Note that mantises prefer to feed upside down, but coordinates are vertically flipped in image processing and kinematic processing, which does not affect the resulting kinematics. (E) Typical kinematics (based on the video stills shown in A–C and Movie 1) of the angles of the joints throughout the strike. Points represent raw angles; black lines represent smoothed angles based on a 10th-order polynomial; dashed red line corresponds to prey capture. (F) Angular velocity based on the smoothed angular data (black lines in E). Dashed red line represents prey capture.

Table 1. Mean trait values and coefficients of variation (CV) for kinematic traits used in this study for each individual mantis (*Phyllocrania paradoxa*)

Individual	Approach time (s)	Sweep time (s)	Approach coxa angle (deg)	Max. coxa angle (deg)	Approach coxa velocity (deg s⁻¹)	Max. coxa velocity (deg s⁻¹)	Approach femur angle (deg)	Max. femur angle (deg)	Approach femur velocity (deg s⁻¹)	Max. femur velocity (deg s⁻¹)	Approach tibia angle (deg)	Max. tibia angle (deg)	Approach tibia velocity (deg s⁻¹)	Max. tibia velocity (deg s⁻¹)	Body displacement (cm)	Foreleg displacement (cm)	Prey distance (cm)
Mean trait value																	
1[a]	0.0273	0.0099	29.69	57.50	1843.2	3249.1	9.28	78.29	975.8	9700.3	34.85	59.85	3732.1	13,831.4	0.13	0.99	1.08
2[b]	0.0255	0.0095	28.89	52.61	1549.7	3447.1	5.84	80.41	675.9	9502.3	41.49	69.40	4671.8	14,367.7	0.12	1.07	1.18
3[a]	0.0293	0.0083	37.78	59.07	2070.0	3804.9	10.90	79.34	904.0	10,551.5	50.79	71.62	4136.5	17,181.4	0.09	0.90	1.01
4[a]	0.0179	0.0081	31.54	57.73	2706.8	4812.5	7.29	82.01	984.5	12,562.1	48.45	70.14	4896.2	16,463.7	0.11	1.03	1.08
5[a]	0.0176	0.0104	30.42	63.84	2324.9	3516.5	7.88	81.32	835.9	9608.1	44.13	75.72	3790.1	16,936.0	0.09	1.03	1.04
6[c]	0.0143	0.0088	22.58	44.60	2143.9	3700.0	5.32	67.29	824.9	10,211.4	37.91	62.62	4574.1	13,557.6	0.07	0.95	1.03
7[a]	0.0179	0.0089	26.16	54.07	1965.4	4090.2	6.43	80.52	936.4	11,152.8	40.45	64.50	4791.7	14,743.9	0.06	0.96	0.99
8[a]	0.0168	0.0086	25.25	53.26	2472.3	3765.2	6.00	78.80	918.7	10,230.4	32.17	63.82	4789.8	13,845.1	0.08	1.09	1.13
CV																	
1	0.615	0.336	0.240	0.140	0.266	0.199	0.310	0.131	0.253	0.222	0.235	0.122	0.214	0.134	0.873	0.093	0.234
2	0.302	0.145	0.139	0.099	0.282	0.214	0.348	0.040	0.378	0.087	0.154	0.128	0.073	0.259	0.389	0.078	0.200
3	0.263	0.240	0.145	0.117	0.206	0.176	0.330	0.123	0.251	0.143	0.245	0.154	0.244	0.121	0.336	0.067	0.116
4	0.640	0.232	0.204	0.190	0.216	0.200	0.396	0.125	0.210	0.108	0.099	0.082	0.191	0.113	0.709	0.086	0.199
5	0.324	0.241	0.202	0.083	0.154	0.149	0.245	0.075	0.238	0.113	0.223	0.052	0.217	0.108	0.521	0.079	0.164
6	0.377	0.195	0.255	0.061	0.108	0.271	0.417	0.163	0.146	0.174	0.352	0.054	0.349	0.204	0.579	0.108	0.153
7	0.396	0.204	0.228	0.096	0.240	0.152	0.251	0.132	0.279	0.148	0.303	0.051	0.251	0.212	0.521	0.108	0.150
8	0.438	0.366	0.259	0.224	0.320	0.186	0.260	0.157	0.214	0.134	0.221	0.121	0.229	0.194	0.661	0.160	0.217

Each mean and CV is based on four to eight feeding strikes per individual.
[a]Eight strikes.
[b]Six strikes.
[c]Four strikes.

coincides with tibia flexion (Fig. 1D, Movie 1). We obtained raw angles for each joint and then smoothed the raw data using a 10th-order polynomial similar to a previous study (deVries et al. 2012; and see Fig. 1E). From the smoothed angular data, we then obtained standardized angles for all joint angles during the strike. Standardized angles were obtained by correcting the angles of each joint for the initial angle at which the forelegs were held by subtracting the angle of each joint at each time step minus the minimum angle of each joint. We then obtained the peak angles as 95% of the maximum standardized angle. We defined the start of a joint moving as 5% of the maximum angle, which was used to calculate the time to peak angle, from 5 to 95% of the maximum angle, similar to a study on fish cranial kinematics (Oufiero et al., 2012). We calculated angular velocities as the derivative of the relative smoothed angle over time. Because all of the movements we examined and digitized were in reference to other body parts, we did not have to subtract out body movement. For example, coxa angular velocity is the change in angle of the prothorax–coxa joint as obtained from points 6, 1 and 2, so body movement is accounted for in the estimation. Maximum velocity for each joint was classified as the maximum instantaneous velocity. Body velocity was calculated separately based on the movement of the line between points 1 and 6 through space. We first obtained the displacement of the body at each time point by calculating the distance moved for a point in the middle of the line between points 1 and 6. We next obtained smoothed body displacement distance using the 10th-order polynomial. We then obtained the derivative of the smoothed body displacement over time to calculate velocity.

To obtain the time of the approach and the sweep, we used the 5% peak coxa angle as an indication of when the strike was initiated. The end of the approach was classified as the time at which the femur was at 10% maximum velocity. Inspection of several videos ensured this was a reliable way to estimate the end of the approach. We used 10% of the femur velocity because that segment is the primary mover in the sweep. Approach time was therefore the difference in time between 5% of coxa angle and 10% of femur velocity. Sweep time was estimated as the difference in time from 10% of femur velocity to the time of prey capture. The approach time was also used to determine the angles at the end of the approach and the maximum velocities of the joints during the approach. These were used for comparison with the maximum angles and velocities achieved during the strike and determine their relationship to prey position. The angles at the end of the approach were obtained by taking the angle of each joint at the frame in which 10% of femur velocity occurred. The maximum velocities represent the instantaneous, maximum smoothed velocity during the approach time (10% femur velocity to prey capture). For both 5% coxa angle and 10% femur velocity, we found the last frame in the time series that was less than each of those values. While these values are not actually the 5 or 10% of the maximums, they represent the frame prior to those traits being greater than 5 or 10%.

Lastly, we obtained an estimate for how much of the foreleg is used during the strike versus how much of the body is used during the strike. To do this, we first calculated the total foreleg expansion, which is the displacement of the tip of the tibia (point 4) from the insertion of the coxa on the prothorax (point 1), giving a total foreleg expansion. Foreleg expansion was then divided by the predator–prey distance [prey (point 7) to coxa/prothorax (point 1), taken at the start of digitization, which is a few frames before movement]. To estimate the percent of lunge used, we divided total displacement of the body by the predator–prey distance. Body displacement is calculated differently than foreleg displacement

because it is in reference to the background, whereas foreleg is in reference to the body, taking into account body movement.

Statistical analyses

We used the CV to determine the amount of stereotypy in components of the strike. Several cut-offs have been proposed for a stereotypic trait (e.g. a CV <1 or between 0 and 20%; Marras et al., 2011; Rice and Westneat, 2005); however, stereotypy is also a relative term, allowing for a comparison among traits (Wainwright et al., 2008). Therefore, we generally accept any trait that is less than 20% to be stereotyped. We also use it relatively to compare components of the strike: those with a lower CV are considered a more stereotypic response. Similar to a previous study (Rice and Westneat, 2005), we take the CV for each trait for each individual (Table 1) and then obtain a mean±standard error of the CV among individuals. This approach takes into account any individual differences. To examine the relationships among kinematic variables and predator–prey position, we used Pearson's correlation coefficient with a two-tailed P-value among each of the 58 strikes. For each set of correlations, we used a Bonferroni correction of the P-values to correct for multiple correlations. All kinematic and statistical analyses were performed in R v3.1.3 (http://www.R-project.org/).

RESULTS

Kinematic patterns

The juvenile mantises used in this study had kinematic patterns of movement similar to those found in previous studies on adults (Corrette, 1990; Prete and Cleal, 1996). In short, the strike was initiated after the mantises targeted the prey item, and began with extension of the coxa and the tibia, holding the femur relatively stationary (Fig. 1 and see Movies 1, 2). This is classified as the approach stage (Fig. 1A). Next, once the coxa was extended and elevated and the tibia was extended, the femur quickly extended, with tibia flexion happening at the same time or shortly after, when the prey was within the prey-capture space. During tibia flexion, the coxa and femur continued to extend, along with the body (Fig. 1). Shortly after the prey was captured, the mantises retracted all limbs to bring the prey in for processing (Movies 1, 2).

At the start of the strike there was variation in the angles and amount of stereotypy of each of the foreleg segments. The mean coxa starting angle was 13.20 deg among all trials, with a mean CV among mantises of 0.481±0.071; the mean femur starting angle was 8.97 deg and was more stereotyped with a mean CV of 0.268±0.023. Finally, the mean starting tibia angle was greater than the other joints at 25.71 deg and was even more stereotyped with a mean CV of 0.169±0.019. Because of the variation in the starting angles, we examined whether these starting angles were correlated to the standardized angles at the end of the approach and the maximums. That is, does the starting position of the mantis affect how much it extends each of its segments? After Bonferroni correction, we found that only the starting angle of the tibia was negatively correlated with the tibia angle at the end of the approach ($r=-0.396$, $P=0.012$). The more the tibia was extended prior to the initiation of the approach, the less the mantis had to extend its tibia during the actual strike. Furthermore, we examined whether the starting angles, which represent pre-strike movement, were correlated with predator–prey position, and found that only that of the coxa was significantly related to predator–prey distance ($r=0.45$, $P=0.0024$) and prey angle ($r=0.60$, $P<0.001$). These results suggest the pre-strike movements of the coxa are more variable and may set up the entire strike as it is related to predator–prey position.

Are strikes stereotypic? Approach versus sweep

Comparing the time during the approach versus the sweep (Fig. 2A), we found that both were more variable than what has been
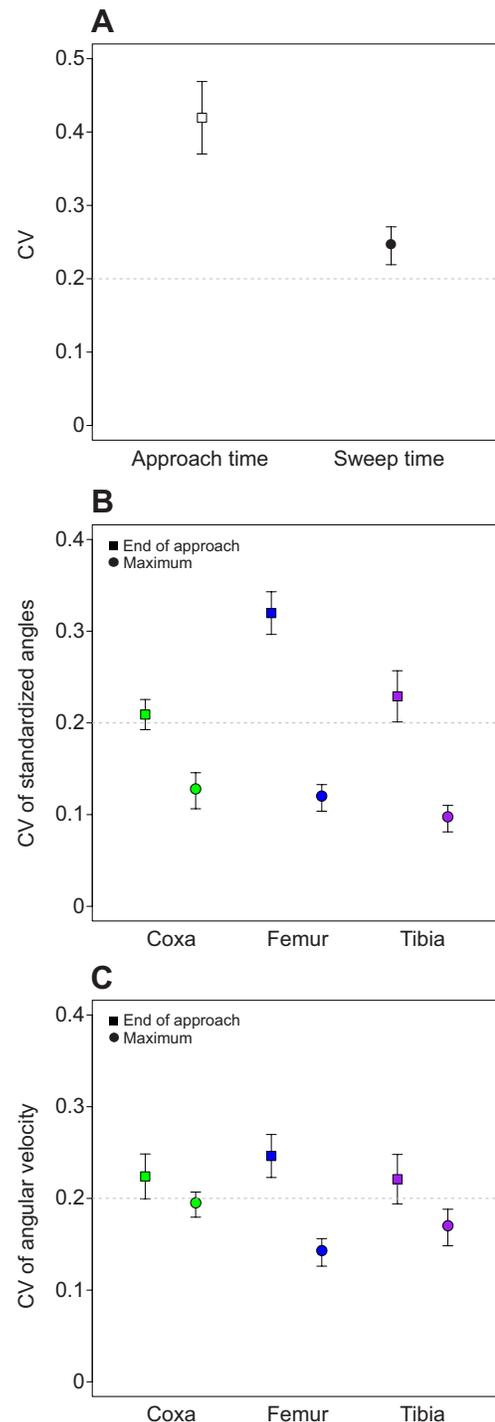

Fig. 2. Coefficients of variation (CV) for strike kinematics. Each point is the mean±s.e.m. CV among the eight mantises (Table 1). CV values below the dashed line at 0.2 have been considered stereotypic. (A) CV for the time to the end of the approach and the time of the sweep phase of the strike. (B) CV values for standardized angles of each joint (coxa, green; femur, blue; tibia, purple) at the end of the approach (squares) and the maximums that occur during the sweep (circles). (C) CV values for smoothed angular velocities of each joint (coxa, green; femur, blue; tibia, purple) at the end of the approach (squares) and the maximums that occur during the sweep (circles).

considered stereotypic, but that the sweep time (CV=0.245±0.026) was more stereotypic than the approach time (CV=0.420±0.049). Among the 58 trials, the sweep time averaged 9.05±0.3 ms whereas the approach averaged 21.09±1.4 ms. Based on this, there is support for the sweep being a more stereotyped response compared with the approach among these mantises, even though both timings are more variable than what has been considered stereotypic.

The maximum angles, which are achieved during the sweep, are also more stereotypic than the angles at the end of the approach, and fall within the range of what has been considered stereotypic (Fig. 2B, Table 1). The maximum coxa, femur and tibia angle mean CVs are all less than 20%, with the maximum tibia angle being less than 10%, whereas the average CV for the angles at the end of the approach are all greater than 20%. Comparing angles, the femur reaches the greatest maximum, followed by the tibia and the coxa; however, at the end of the approach, the tibia reaches the greatest angle, followed by coxa and the femur (Table 1).

Results for the variation in angular velocity of the joints were similar to those for the angles (Fig. 2C, Table 1). First, it was hypothesized that the flexion of the tibia should be more stereotypic than the extension of the coxa and the femur. We did not find support for this hypothesis as the CV for the maximum tibia velocity, which occurs during the flexion in the sweep, was similar to the CV for the coxa and femur maximum extension velocity, which were all less than 20%, suggesting that they are all stereotypic (Fig. 2C). Second, consistent with the variation in angles, the maximum velocities were more stereotypic compared with the maximum velocities during the approach, although the difference between coxa angular velocity CVs was minimal (Fig. 2C). Lastly, the extension of the tibia during the approach and the flexion of the tibia in the approach had the greatest velocities compared with the velocity of the other joints.

Predator–prey position and velocity

Comparing predator–prey distance with the maximum instantaneous velocities of the approach, the sweep and the body, we found no significant relationships of any velocity with predator–prey distance after Bonferroni correction. In relation to predator–prey angle, we found a significant positive correlation with the velocity of the coxa during the approach (r=0.35, P=0.046; Fig. 3A) and a significant negative correlation with maximum femur angular velocity, which occurs during the sweep (r=−0.37, P=0.027; Fig. 3B). Therefore, mantises do not seem to strike faster when the prey is farther away. Another way to examine the speed of strikes is to examine the time to key events, such as time to peak angles, approach time or sweep time. When examining the relationship with predator–prey distance, it is only significantly positively related to the sweep time, suggesting the farther the mantis is from the prey, the longer the sweep (r=0.67, P<0.001; Fig. 3C), which does not lend support for faster strikes on prey farther away. Furthermore, predator–prey angle was not significantly related to the time to peak angles for any of the segments (all P>0.05).

Approach and sweep angles in relation to predator–prey position

We examined the relationship between the distance of the prey and the angle of the prey in relation to the angles of each joint at the end of the approach and the maximum angles achieved to determine whether the mantises are modulating their kinematics. After Bonferroni correction, we found that only the maximum coxa angle achieved was significantly positively related to predator–prey distance (r=0.45, P=0.002) and both the coxa angle at the end of the

approach (r=0.41, P=0.009) and the maximum coxa angle (r=0.54, P<0.001) were related to predator–prey angle. The farther or higher the prey item, the more the coxa is extended. No other joints were significantly related to predator–prey distance or angle. If the
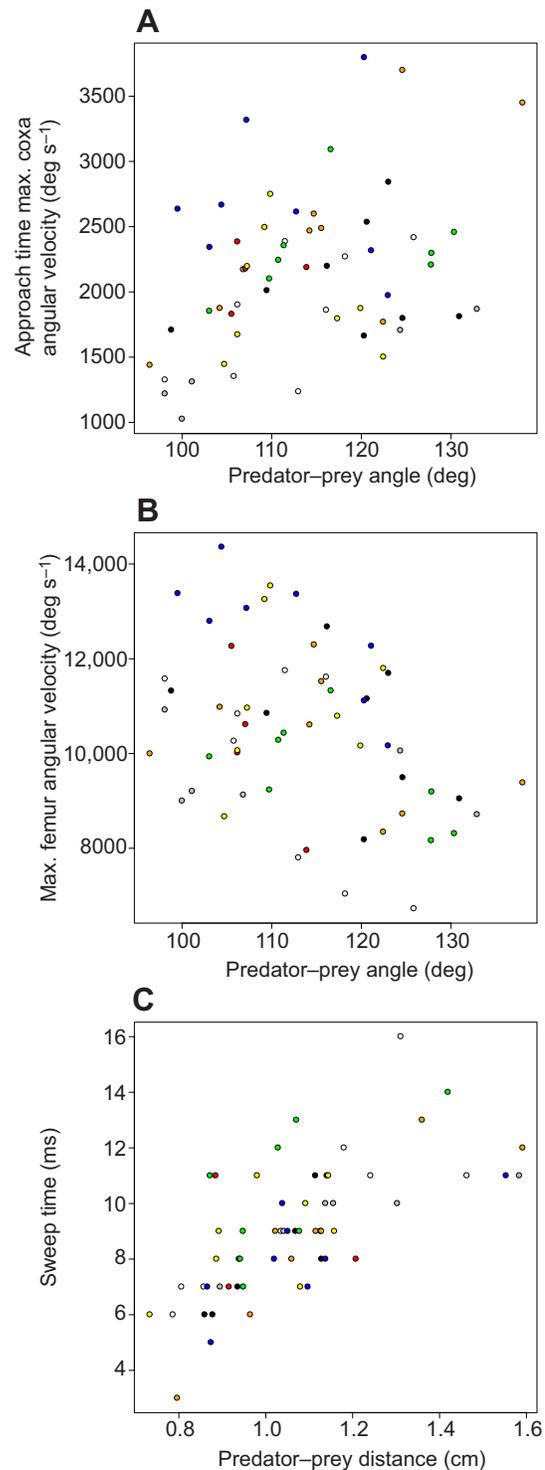

Fig. 3. Relationships between predator–prey position and strike kinematics. Each point represents an individual feeding strike; colors represent individuals. (A) Velocity of the coxa–prothorax joint during the approach was significantly positively related to predator–prey angle (r=0.35, P=0.046). (B) Maximum femur angular velocity was significantly negatively related to predator–prey angle (r=−0.37, P=0.027). (C) Mantises took longer during the sweep when the prey was farther away (r=0.67, P<0.001).

kinematics of the mantises are stereotypical, they may vary their approach time to set up their forelegs for the sweep. To determine whether this is occurring, we correlated the approach time with the angles at the end of the approach and the maximum angles, and found significant positive correlations between approach time and the angle of the coxa and femur at the end of the approach (coxa $r=0.601$, $P<0.001$, femur $r=0.597$, $P<0.001$), but no other significant correlations.

Foreleg versus body movement

Lastly, we examined the amount of stereotypy in the amount of foreleg used versus the amount of body used during strikes and examined the relationships of each with predator–prey position. First, we found more stereotypy in the percentage of foreleg used (CV=0.088±0.008) to close the distance between predator and prey, and the total foreleg displacement during the strike (from point 1 to point 4, CV=0.097±0.010), compared with the percentage (CV=0.459±0.053) and displacement of the body (CV=0.574± 0.061; Fig. 4). These findings are not surprising given that the foreleg is a fixed length compared with the use and movement of the mesothoracic and metathoracic legs in the strike.

Examining the relationship of foreleg and body usage in relation to predator–prey position, we found a significant negative relationship between predator–prey distance and the percentage of foreleg used in the strike ($r=-0.73$, $P<0.001$; Fig. 5A) and a significant positive relationship between predator–prey distance and the amount of lunge used in the strike ($r=0.50$, $P<0.001$; Fig. 5B). However, we also found significant positive relationships between predator–prey distance and total foreleg expansion and body displacement (foreleg $r=0.46$, $P=0.003$; body $r=0.71$, $P<0.001$). There is no significant relationship between the percent of foreleg used and foreleg expansion ($P>0.05$), but there is a significant negative relationship between the percent of foreleg used versus the percent of body used ($r=-0.38$, $P=0.029$; Fig. 5C). These results suggest that although the mantises extend their forelegs more when prey are farther away, that percentage use of forelegs decreases with prey distance, which is compensated for by increasing their body
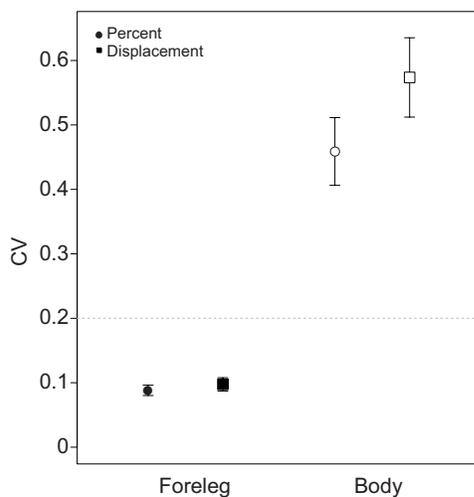
use, i.e. more lunge. Therefore, the mantises are modulating their strikes by using more, but not faster, body movements when prey are farther away. After Bonferroni correction, we found no significant
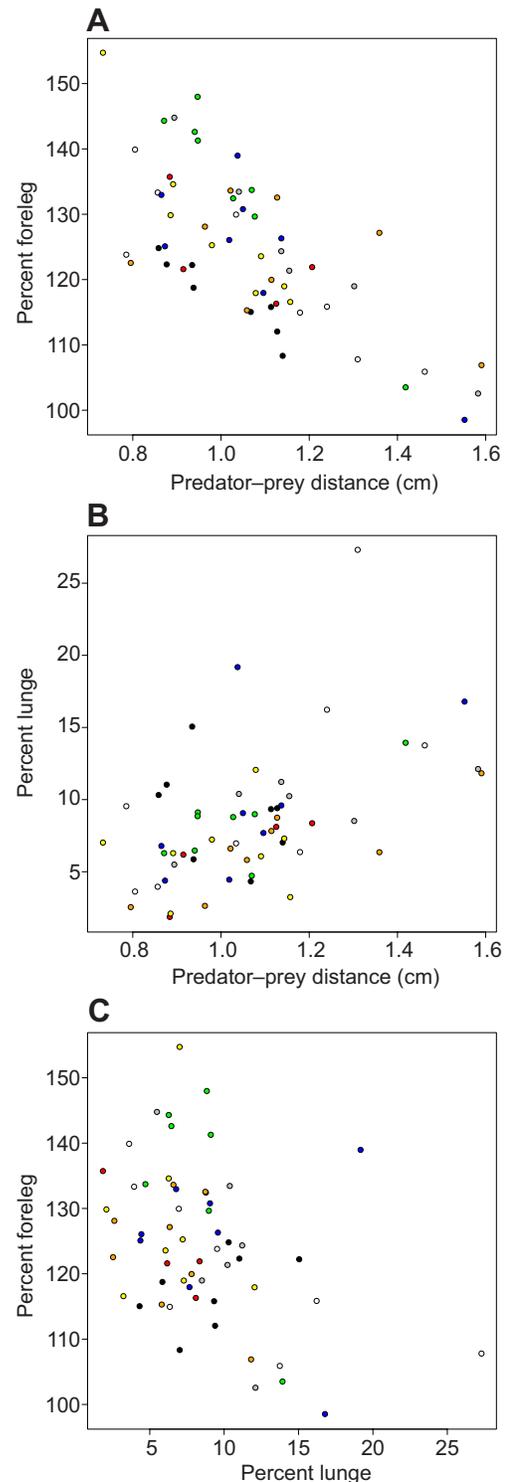
Fig. 4. CVs for the amount of foreleg and body used in the strikes. Points represent mean±s.e.m. CV strike kinematics among the eight mantises (Table 1). CV values below the dashed line at 0.2 have been considered stereotypic. The percent used (taken as the percent of the foreleg or body used to close the predator–prey distance) is represented by the circles, the actual displacements are the squares. Results were consistent for each method of estimating how much foreleg or body was used.

Fig. 5. Percent foreleg and body (lunge) used in relation to predator–prey distance and each other. Each point represents an individual feeding strike; colors represent individuals. (A) The farther away the prey, the less the foreleg was used to close the predator–prey distance ($r=-0.73$, $P<0.001$). (B) The farther away the prey, the more the body was used to close the predator–prey distance ($r=0.50$, $P<0.001$). (C) The more body used, the less foreleg used ($r=-0.38$, $P=0.029$).

relationship between predator–prey angle and the percent or displacement of the foreleg or lunge used in the strike (*P*>0.05).

DISCUSSION
Stereotypy in feeding kinematics
Like many feeding functional systems, the feeding strikes of praying mantises involve the complex movements of several different components to close the distance between predator and prey. Similar to previous results (Corrette, 1990; Maldonado et al., 1967; Prete and Cleal, 1996), we found consistent motor patterns of the strike, with the initial extension of the coxa and tibia, followed by the rapid extension of the femur and flexion of the tibia (Fig. 1, Movies 1, 2). Our results suggest that the kinematics and timing of the sweep are more stereotyped than the kinematics and timing of the approach. Furthermore, our results suggest that although the kinematics of the femur and tibia are stereotyped and not related to prey position, feeding strikes in praying mantises may be modulated by adjusting the angle of the coxa with the prothorax and the amount of lunge used during the strike (movement of mesothoracic and metathoracic legs). Previous studies have suggested that the strike of the praying mantis is not stereotypical, as there is a range of prey positions that elicit a strike (Corrette, 1990; Prete and Cleal, 1996). However, these studies did not examine the amount of variation in each of the morphological components responsible for the strike (e.g. coxa, femur, tibia, approach or sweep).

Some have suggested that the praying mantis feeding strike is not stereotypical because of the variation in the lunge component (Copeland and Carlson, 1979; Prete and Cleal, 1996; Prete et al., 1990). Our results agree with this previous assessment in that there is more variability in the lunge compared with the percent of the forelegs that is used in the strike (Fig. 4). Given the morphological constraints of the forelegs based on their size, the lunge, which is due to the movement of the mesothoracic and metathoracic legs, can compensate for the foreleg size limitations to produce a greater range (distance and angles) of capture zones. In fact, the percent of lunge used in a strike increased positively with prey distance (Fig. 5B), similar to previous studies. If components of the strike are stereotypic, as our data suggest, the lunge may help 'steer' the forelegs to successfully capture the prey, as suggested previously (Corrette, 1990). Given the variability in this trait, there may be sensory feedback to these appendages to adjust the position of the striking forelegs; however, to further disentangle these effects, more detailed analyses are needed (Kagaya and Patek, 2016).

There is mixed evidence for the stereotypy of prey capture in other groups of organisms. Early hypotheses suggested that aspects of prey capture might be stereotyped based on prey specialization, limitations of muscular and skeletal systems, or because of the rapid movement of the often integrated prey-capturing apparatus. For example, Rice and Westneat (2005) found consistent and stereotypic patterns of movement for many kinematic traits (e.g. maximum gape, maximum velocity and maximum eye movement) both within and between two species of parrotfish. While there are limitations to inferences from two-species comparative studies (Garland and Adolph, 1994), the results from Rice and Westneat (2005) suggest consistent kinematics in the two species studied, which differed in feeding ecology but were fed the same items in the study. Similarly, Reilly (1995), found little change in the feeding kinematics of salamanders (*Salamandra salamandra*) across ontogeny. Conversely, Montuelle et al. (2012) found flexibility in the strikes of a varanid lizard, with mobile prey such as live crickets and adult mice eliciting similar kinematics compared with strikes on non-mobile prey.

Among invertebrates, Kagaya and Patek (2016) found variation in the ballistic strikes of smashing mantis shrimp. Because these shrimp use a power-amplified system to rapidly move the striking appendage, the nervous system may not be able to control it once it has been initiated. However, despite this ballistic trait that occurs too fast for neuronal modulation, Kagaya and Patek (2016) found that the mantis shrimp can vary the velocities by adjusting pre-strike contraction of the muscles. Furthermore, research on the stereotypy of extensor contraction during walking in the stick insect *Carausius* sp. demonstrates variability during a rhythmic neural pattern (Hooper et al., 2006). This is particularly interesting as mantises also use their forelegs for locomotion (Loxton and Nicholls, 1979). Although the kinematics of the sweep phase of the strike are stereotypic, it would be interesting to determine whether the same, or more, variation exists while walking in praying mantises, integrating locomotion and feeding (Kane and Higham, 2015). Based on the above results, there does not seem to be consistent consensus on whether the feeding strikes of animals are, or should be, stereotyped or flexible. Our results, along with some others (Reilly, 1995; Rice and Westneat, 2005), suggest stereotypy in components of feeding strikes, whereas others highlight the amount of variability (Kagaya and Patek, 2016; Montuelle et al., 2012), even in stereotypic motor activation patterns.

The stereotypic patterns of some of the kinematic traits in our study may be due to a low variability of prey position. Each prey was introduced to the mantis and moved to elicit tracking and eventually the strike. Previous results have shown variation in strike initiation in relation to predator–prey position (Corrette, 1990; Prete and Cleal, 1996). We moved the prey to obtain a range of strike positions, but despite this initial movement of the prey, there was still low variability in both predator–prey distance (CV=0.174) and angle (CV=0.096). However, despite this low variability in prey position, we still see variation in some aspects of the strike in relation to prey position (Figs 3, 5). It is also unclear whether the low variability in predator–prey position reflects low variability in where the mantis forelegs can capture prey or where prey are eliciting a strike (see below). Mantises may prefer to strike when prey are 'in range', but it is not clear whether the visual system constrains the feeding strike or whether the feeding appendage constrains the strike. More specifically, it is not clear whether the mantis visual system, with variation in depth perception, is responsible for determining what prey positions the mantis will elicit a strike or whether the length of the forelegs limit where a mantis can strike. However, recent work has shown variation in strikes in relation to the 'perceived' prey target (Nityananda et al., 2016a,b). Given the behavioral modifications of both of these systems ['peering' to enhance depth perception (Kral and Poteser, 2009) and lunge to enhance strike distance], it may be that the two systems are co-evolving to ensure successful capture of prey items; that is, the greater the depth perception of a species, the longer their forelegs. However, these relationships have not been explored on a macroevolutionary scale in mantises.

Kinematics and predator–prey position
One of the hypotheses we set out to test was a relationship between strike speed and prey distance, with the prediction that the farther away the prey, the faster the strike. This relationship has been observed in fish feeding, with species that strike from farther distances using faster body speeds to close the predator–prey gap (Oufiero et al., 2012). We found no relationship of predator–prey position and velocities of the joints, except a significant positive relationship with coxa velocity during the approach and prey angle

(Fig. 3A). Even though our prey were alive and moved in front of the mantises, they were not as evasive as other studies of feeding kinematics (Longo et al., 2016; Montuelle et al., 2012; Oufiero et al., 2012). Therefore, changes in the velocity of the prey of the praying mantis may elicit more variation in the stereotyped kinematic traits we observed. While the strikes of praying mantises have been observed in relation to prey position, few have examined the detailed kinematics in relation to variation in prey velocity.

Examining the angles at the end of the approach and maximum angles, we found that coxa angle at the end of the approach and the maximum reached during the sweep were significantly positively related to prey angle, and the angle of the coxa at the end of the approach was also positively related to predator–prey distance. These joint angles may be altered as a result of a change in predator–prey distance to ensure prey capture, as has been found in other species of mantis. For example, Corrette (1990) examined the angles of each joint during the capture position in unrestrained *Tenodera aridifolia sinensis* mantises. Our measures of prey distance and angle are the same, but he found a significant positive correlation between coxa and femur angle and prey distance, a significant negative correlation between tibia angle and prey distance and a significant positive correlation between coxa angle and prey angle (similar to our results). While most of these results differ from ours, it may be due to the angles of the joints that were obtained. We obtained the angle of the joints at the end of the approach and the maximum reached during prey capture. Corrette (1990) only reports the angles at the capture position, which is when the prey makes contact with the mantis, and these may not be the maximums achieved. Furthermore, we corrected the angles for their initial position to obtain an idea of how much they move; Corrette did not do this, but instead shows significant relationships of joint angles 175–180 ms prior to tibial capture in restrained mantises only. Lastly, the differences in our results with previous results could be due to differences in the lifestyle of the mantises analyzed. Although both *P. paradoxa* and *T. aridifolia* are classified as ambush predators (Svenson and Whiting, 2004), there may be differences in the prey they are selecting, which could lead to differences in their sensory systems, musculoskeletal traits and, ultimately, kinematics. However, comparisons of strike kinematics in mantises varying in diet and lifestyle have not been explored. Therefore, the differences in our kinematic results from previous results could represent the slight differences in kinematics analyzed, methods, mantis species or age (adults were used in Corrette's study, whereas we used juveniles). However, taken together, these results suggest that the coxa–prothorax angle seems to be one of the more important traits the mantises may use to adjust for prey position, as both our study and Corrette's found correlations of this trait with prey position, both prior to the approach and during the strike. The flexibility of this joint is in congruence with observations of its anatomical features in other species of mantises; as noted by Frantsevich (1998), 'the front coxa of a praying mantis is extremely versatile'. It is currently unclear whether the angles of the other joints are important for modulating strikes based on prey position.

Similar to previous studies (Corrette, 1990; Maldonado et al., 1967), we controlled for prey size to remove variation in this trait. However, the angles of the joints in mantises may be modulated in relation to prey size as well as position. For example, larger prey items may elicit greater angles of the joints (particularly the femur–tibia joint) to ensure successful capture. However, this may not be the case in *P. paradoxa* as they have been observed to capture small, uniformly sized prey items. Nevertheless, few studies have examined the relationship of prey size on strike kinematics,

although behavioral studies suggest the modification of behavior (i.e. proportion of strikes) is based more on prey distance than size (Nityananda et al., 2016a,b; Prete et al., 2013). Loxton and Nichols (1979) even modeled the optimal prey size that should elicit striking behavior, but not the associated kinematics. To fully understand the relationship of prey size and position with strike kinematics, more controlled experiments of precise prey size and positions, varying in both distance and angle, are warranted.

Strike kinematics and vision

Praying mantises have become models for vision research as they are one of the few insects that have the ability for binocular vision. The integration of the visual system may be related to the feeding appendages to ensure successful capture of prey items. For example, it has been suggested that mantises can perceive depth at 25 mm (Rossel, 1980, 1983), and recent work has shown that female *Sphodromantis lineola* strike most often when prey are perceived to be at this depth (Nityananda et al., 2016b). In our juveniles, the mean (±s. e.m.) distance they struck at the prey was 10.9±0.025 mm, with a range of 7.3–15.9 mm. Although this is not a measure of depth perception, it falls well below the 25 mm suggested, and may be related to ontogenetic stage or placement of the eyes in this species (Kral and Poteser, 2009). Intra- and interspecific variation in depth perception has not been examined in detail (Kral and Poteser, 2009), but may be related to the morphology and kinematics of the striking appendages. Furthermore, Rossel (1980, 1983) found that the praying mantis *Tenodera australasiae* can infer both position of the prey and velocity of the prey. We examined the relationship of kinematics with prey position and found very few significant correlations. However, our prey were immobile and not moving as much as natural prey, as they were moved randomly in front of the mantis to elicit a strike, not flying by like a natural prey item. We found very few correlations of angular speeds of the forelegs with other aspects of the strike, such as predator–prey position, lunge time and sweep time. Aspects of the kinematics of the strike may be related to velocity of the moving prey as well as its position; faster strikes may be elicited by a faster moving target to ensure successful capture of the prey item. Many studies have examined the relationship of varying visual targets with strike response (e.g. Prete et al., 2013), but few have investigated patterns of kinematic variation associated with varying visual stimuli. The integration of these two functional systems (vision and feeding) may provide insight into the coordination of the systems, feedback control in the systems, modulation of the feeding strikes and evolutionary relationships between the eyes of praying mantises and their raptorial feeding appendage.

Praying mantises are one example of a group of invertebrates that have independently evolved exaggerated, raptorial appendages to capture prey (Anderson and Patek, 2015; deVries et al., 2012; Kral et al., 2000; Lavine et al., 2015; Patek et al., 2004). Through the rapid, coordinated movements of the enlarged raptorial forelegs, cryptic mantises can successfully capture unsuspecting prey. Our results suggest stereotypic kinematics during the sweep, with flexibility in the coxa–prothorax joint and lunge to help close the predator–prey distance. However, our results are based on juveniles within one cryptic species. It remains to be seen whether these patterns of kinematic variation are similar across ontogenetic stages and across the diversity of praying mantises.

Competing interests

The authors declare no competing or financial interests.

Author contributions

C.E.O. and T.N. designed the study, T.N., A.S and A.E. collected the data, and C.E.O. analyzed the data and wrote the manuscript with comments from T.N., A.S. and A.E.

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