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RESEARCH ARTICLE

The kinematics of amblypygid (Arachnida) pedipalps during predation: extreme elongation in raptorial appendages does not result in a proportionate increase in reach and closing speed

Callum J. McLean^{1,2}, Charlotte A. Brassey^{2,*}, Michael Seiter^{3,4}, Russell J. Garwood^{5,6} and James D. Gardiner²

ABSTRACT

The link between form and function is key to understanding the evolution of unique and/or extreme morphologies. Amblypygids, or whip spiders, are arachnids that often have highly elongated spined pedipalps. These limbs are used to strike at, and secure, prey before processing by the chelicerae. Amblypygi pedipalps are multifunctional, however, being used in courtship and contest, and vary greatly in form between species. Increased pedipalp length may improve performance during prey capture, but length could also be influenced by factors including territorial contest and sexual selection. Here, for the first time, we used high-speed videography and manual tracking to investigate kinematic differences in prey capture between amblypygid species. Across six morphologically diverse species, spanning four genera and two families, we created a total dataset of 86 trials (9–20 per species). Prey capture kinematics varied considerably between species, with differences being expressed in pedipalp joint angle ranges. In particular, maximum reach ratio did not remain constant with total pedipalp length, as geometric scaling would predict, but decreased with longer pedipalps. This suggests that taxa with the most elongated pedipalps do not deploy their potential length advantage to proportionally increase reach. Therefore, a simple mechanical explanation of increased reach does not sufficiently explain pedipalp elongation. We propose other factors to help explain this phenomenon, such as social interactions or sexual selection, which would produce an evolutionary trade-off in pedipalp length between prey capture performance and other behavioural and/or anatomical pressures.

KEY WORDS: Predation, Pedipalp, Whip spider, Arachnid, Prey capture

INTRODUCTION

For predators, the ability to capture and secure prey is essential for long-term survival. Anatomical and behavioural adaptations that

confer an advantage to the predator during prey capture therefore evolve under strong natural selection (Abrams, 2000). Whilst the evolution of such structures must be considered within the context of feeding, their morphology may also be subject to additional selective pressures (McLean et al., 2018). The size and shape of scorpion chelae, for example, evolve under natural selection for ‘pinch’ force in accordance with their foraging strategy (van der Meijden et al., 2012). Yet scorpion palpal chelae are also under the influence of sexual selection, owing to their use in sexual conflict, courtship and mating, particularly in ‘cheliceral grip’ behaviour prior to mating (Maury, 1975; Polis and Sissom, 1990; van der Meijden et al., 2012).

Likewise, the cheliceral feeding apparatus of spiders is under strong natural selection to puncture the chitinous exoskeleton of prey, but in many species it is also under sexual selection for performance in sexual display and/or contest (Faber, 1983; Costa-Schmidt et al., 2008; Foelix, 2011). For example, male chelicerae are enlarged relative to those of females in spider species where males offer nuptial gifts prior to mating (Costa-Schmidt et al., 2008), and also in species where they are used in sexual conflict (Rovner, 1968; Watson, 1990). In extreme cases, competition for mates can significantly alter the use of chelicerae in prey capture. For example, male *Myrmarachne palataleoides* use their cephalothorax to secure prey, before ‘skewering’ prey items on their enlarged chelicerae, in contrast to females, which secure and envenom prey with the chelicerae. The difference in prey capture behaviour is thought to be due to adaptations arising from male intrasexual competition, with the enlarged male chelicerae having lost the ability to envenom prey (Pollard, 1994).

Beyond arachnids, fiddler crab major claws have also become so exaggerated they are no longer used for feeding (Rosenberg, 2002), and the enlarged canines of sabre-toothed cats also represent a structure where modification due to sexual selection may have had a detrimental effect on prey capture performance (Randau et al., 2013). Thus, a causal link between morphology and prey capture/processing performance in such ‘feeding’ structures may not exist and should not always be assumed. Comparative biomechanical studies of prey capture and processing are essential in order to explicitly test these form–function hypotheses.

The raptorial pedipalps of Amblypygi exemplify such multifunctional structures. Their unique morphology has been assumed to reflect adaptation towards their predatory way of life, whilst also being used in other behaviours. Amblypygi is an order of arachnids comprising over 200 species (Gibbons et al., 2019). Members of the group are distinguished by their elongate ‘whips’, a greatly lengthened and segmented first leg pair with mechanoreceptive and chemoreceptive functions (Igelmund, 1987), and their large raptorial pedipalps, which are used to ambush prey in lieu of the venom or silk of other arachnid orders.

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The pedipalps also function in courtship, territorial contest and grooming (Weygoldt, 2000; Garwood et al., 2017; Seiter et al., 2019). Amblypygi pedipalps are homologous to the claw-bearing limbs of scorpions and pseudoscorpions, and to the limb bearing the palpal bulb used to transfer sperm in male spiders (Weygoldt, 2000). Their pedipalps are elongated relative to those of other arachnids, are heavily spinous, and consist of six anatomical segments, with the more proximal femur and distal tibia comprising the majority of the length (our pedipalp terminology follows Quintero, 1981, throughout). Prey is caught when the amblypygid extends its pedipalps around a prey item and pulls it back towards the chelicerae (Fig. 1), with flexion–extension thought to occur primarily at the femur–tibia joint (Santer and Hebets, 2009; Seiter et al., 2019). The prey is then secured within a ‘prey capture basket’ of terminal palpal spines and processed by the chelicerae.

Amblypygi pedipalps are characterised by high interspecific morphological diversity (Weygoldt, 2000). Across the group, pedipalps vary greatly in both absolute length and length relative to body size. Adult members of the genus *Sarax* and *Charinus* are characterised by pedipalps with a combined femur and tibia length equal to approximately one body length (Rahmadi, Harvey and Kojima, 2010; Jocque and Giupponi, 2012), whilst members of *Euphrynichus* and *Phrynichus* possess pedipalps with combined femur and tibia lengths four times their body length (Simon and Fage, 1936; Weygoldt, 1998, 2000). Spination also varies considerably within the group (Weygoldt, 2000).

Across all amblypygid taxa for which feeding has been documented, the pedipalps play an essential role in prey capture (Weygoldt, 2000). Data on wild feeding behaviour in Amblypygi are entirely observational and scarce, limited to a very small number of species and individuals. Amblypygi have been observed to engage in different prey capture behaviours, with some species preying upon moths in flight (*Heterophrynus batesii*, *Phrynus longipes*, *Paraphrynus parvulus*; Beck and Görke, 1974; Hebets, 2002), others striking at freshwater prawns (*Heterophrynus cheiracanthus*; Ladle and Velandar, 2003), and larger individuals having been observed to take vertebrate prey, including hummingbirds, coqui frogs and anole lizards (*P. longipes*, *Heterophrynus longicornis*; Owen and Cokendolpher, 2006;

Stewart and Woolbright, 1996; Reagan, 1996; Kok, 1998). Other workers have observed necrophagy in amblypygids of the species *Paraphrynus raptator*, *H. longicornis* and *P. longipes* (Trujillo et al., 2021). However, Amblypygi in general are thought to feed mainly on terrestrial invertebrates primarily from the Orthoptera and Blattodea (Chapin and Hebets, 2016). Observations that show amblypygids catching a diverse range of prey strongly suggest that some species have specialised in targeting organisms that differ from the ground-dwelling invertebrates that the palpal prey capture system was probably initially optimised for. These specialisations in novel prey types could lead to a mismatch between recent selection pressures and the deeper history of the prey capture system, complicating form–function relationships in ‘specialist’ species.

Pedipalps are also known to play a part in other amblypygid behaviours. Recent work has demonstrated the importance of pedipalp length in territorial contests. The majority of territorial contests in *P. longipes* are decided by pedipalp display, with the individual possessing the longer pedipalps becoming the victor (Chapin and Reed-Guy, 2017). Pedipalp display is also used in courtship, suggesting that pedipalps may also be under the influence of sexual selection (Weygoldt, 2000). This raises the intriguing possibility that the lengthened pedipalps of Amblypygi may not be optimised for, or fully utilised in, prey capture.

Here, we quantified, for the first time, the kinematics of prey capture in a diverse sample of Amblypygi taxa, with combined pedipalp femur and tibia lengths spanning from less than one to more than three times body length. We use high-speed video to record prey capture events, and motion tracking software to track anatomical landmarks. In doing so, we extracted data for maximum strike speed, maximum reach ratio (maximum reach divided by total pedipalp length) and joint angle ranges across species. No elastic storage mechanism has been documented in the amblypygid pedipalp, and closing motion is assumed to occur entirely through muscle contraction (Seiter et al., 2019). Here, we tested the hypothesis that pedipalp kinematics vary with pedipalp length on the basis of geometric scaling alone. Additionally, we tested whether prey capture uses a common kinematic pattern across species, extending the initial single-species results of Seiter et al. (2019). Specifically, we tested the following hypotheses. (1) Based

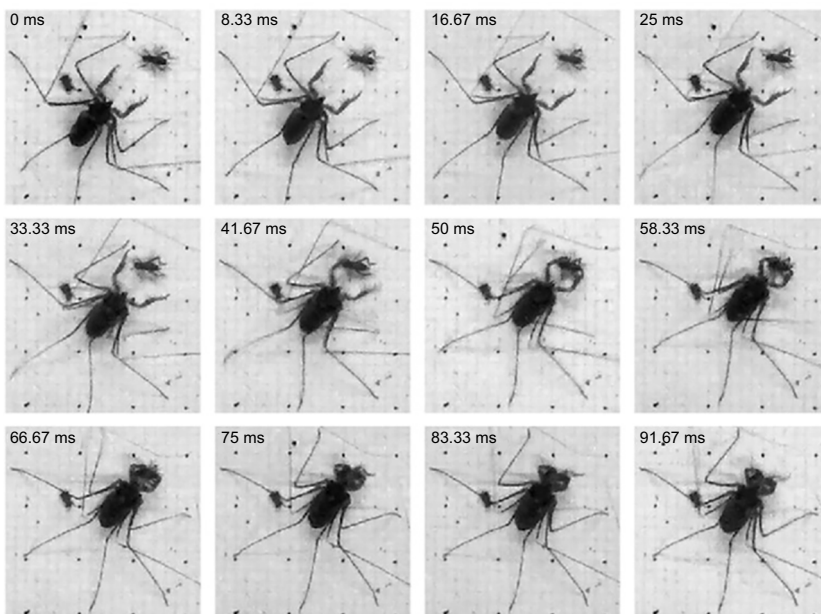


Fig. 1. Example high-speed video frames of prey capture by an *Acanthophrynus coronatus* amblypygid. The amblypygid extends its pedipalps either side of the prey before striking it back towards the chelicerae, securing the prey with the terminal spines in the ‘prey capture basket’.

on previous observational data from Weygoldt (2000), basic kinematic parameters (joint angle ranges, maximum reach ratio and maximum strike speed) will not differ significantly between species relative to pedipalp length. (2) Maximum reach ratio during prey capture will remain constant relative to total pedipalp length. (3) Maximum strike speed during prey capture will remain constant relative to total pedipalp length.

Should these hypotheses be substantiated by the kinematic data, it would suggest that the lengthening of the pedipalp has evolved in amblypygid taxa to facilitate prey capture through increased total reach (N.B. reach ratio will remain constant). If, however, prey capture kinematics differ from the predictions above, the pedipalps may not be solely optimised for prey capture, and could be under additional selective pressures related to territorial contest or courtship. Deviation from these hypotheses could also reflect specialisation for a particular prey type outside ground-dwelling invertebrates.

MATERIALS AND METHODS

Study species, specimens and husbandry

We recorded specimens of six species from four genera and two families in this study: *Phrynus goesii* (Thorell, 1889), *Phrynus barbadensis* (Pocock 1894), *Damon diadema* (Simon 1876), *Damon medius* (Herbst 1797), *Acanthophrynus coronatus* (Kraepelin 1899) and *Euphrynichus bacillifer* (Gerstaecker 1873) (Table 1). The chosen species span a wide range of relative pedipalp lengths (Fig. 2), with *A. coronatus* characterised by total pedipalp lengths (femur, tibia and tarsus) of just over one body length. *Euphrynichus bacillifer* and *D. medius*, in contrast, have total pedipalp lengths of roughly three times their body lengths. All other species fall between these extremes (Table 1).

Taxonomically, the species herein come from the two largest amblypygid families: *P. barbadensis*, *P. goesii* and *A. coronatus* fall into Phrynidae, and *D. medius*, *D. diadema* and *E. bacillifer* are members of Phrynichidae. Both families sit within the most recently branching amblypygid clade, Phyrinoidea (Garwood et al., 2017).

This distinguishes them from *Charon* in which prey capture has been previously studied (Seiter et al., 2019). Within our phrynid genera, *Acanthophrynus* is considered the genus with the most recent origin, having diverged from *Paraphrynus* in the Late Miocene or Early Pliocene, which in turn had previously diverged from *Phrynus* (Schramm et al., 2021). Within our Phrynichidae species, *Damon* is considered to be a branch later than *Euphrynichus* (Prendini et al., 2005). Within *Damon*, *D. medius* is part of the West African group, considered to be earlier branching than the East African group to which *D. diadema* belongs (Prendini et al., 2005). No order-wide genus- or species-level tree yet exists for amblypygids, so the exact phylogenetic relationships between these taxa remain uncertain.

This collection of species also covers a large geographic range, with *P. barbadensis* and *P. goesii* native to the Caribbean Islands, *D. medius* originating from West Africa, *D. diadema* from East Africa, *A. coronatus* from continental North America and *E. bacillifer* from Central Africa (Harvey, 2013).

All individuals used were adults and were unsexed. Amblypygi pedipalps are sexually dimorphic in both length and shape (McLean et al., 2020). In the present study, length was directly incorporated into the analysis. Shape dimorphism (typically present in spination of the pedipalp) is unlikely to impact upon opening–closing dynamics. Specimens of *D. medius* and *D. diadema* were acquired through the pet trade; *D. medius* were originally wild caught in Nigeria, and *D. diadema* were captive bred. *Phrynus barbadensis*, *P. goesii*, *A. coronatus* and *E. bacillifer* were captive bred from a population kept by M.S. When introduced into our care, individuals were housed separately in 395 mm×255 mm×290 mm clear plastic boxes. Individuals were fed two crickets weekly; smaller individuals were fed smaller crickets. Animals were housed and trials were conducted at 26–27°C and 55–60% humidity.

This study adheres to the ASAB/ABS guidelines for the use of animals in research, the current legal requirements for

Table 1. General information and basic morphological measurements of individuals of the six Amblypygi study species

Species	Family	Occurrence	N	Total trials	ID	Individual trials	Body length (mm)	Pedipalp length (mm)	Pedipalp length/body length	Acquisition
<i>Phrynus barbadensis</i>	Phrynidae	Caribbean	2	17	PB_1	7	18.9	24.2	1.3	Captive bred (M.S.)
					PB_2	10	20.0	23.5	1.2	
<i>Phrynus goesii</i>	Phrynidae	Caribbean	2	11	PG_1	8	21.0	26.8	1.3	Captive bred (M.S.)
					PG_2	3	21.9	25.1	1.2	
<i>Acanthophrynus coronatus</i>	Phrynidae	North America	5	9	AC_1	2	27.7	32.9	1.2	Captive bred (M.S.)
					AC_2	1	27.8	35.1	1.3	
					AC_3	4	27.3	31.7	1.2	
					AC_4	1	25.2	28.0	1.1	
					AC_5	1	26.0	26.6	1.0	
<i>Damon diadema</i>	Phrynichidae	East Africa	4	20	DD_1	6	17.5	44.3	2.5	Captive bred (pet trade)
					DD_2	4	19.7	32.7	1.7	
					DD_3	3	18.3	33.7	1.8	
					DD_4	7	20.3	41.9	2.1	
<i>Euphrynichus bacillifer</i>	Phrynichidae	Central Africa	3	9	EB_1	5	19.3	62.2	3.2	Captive bred (M.S.)
					EB_2	2	19.7	65.6	3.3	
					EB_3	2	18.6	47.6	2.6	
<i>Damon medius</i>	Phrynichidae	West Africa	7	20	DM_1	6	28.4	74.1	2.6	Wild caught (pet trade, Nigeria)
					DM_2	2	30.4	103.0	3.4	
					DM_3	2	26.3	75.9	2.9	
					DM_4	3	29.0	94.2	3.3	
					DM_5	4	26.2	89.7	3.4	
					DM_6	2	30.5	102.4	3.4	
					DM_7	1	26.1	75.0	2.9	

Pedipalp length is the combined length of the femur, tibia and tarsus (average of left and right for each individual). N, number of individuals.

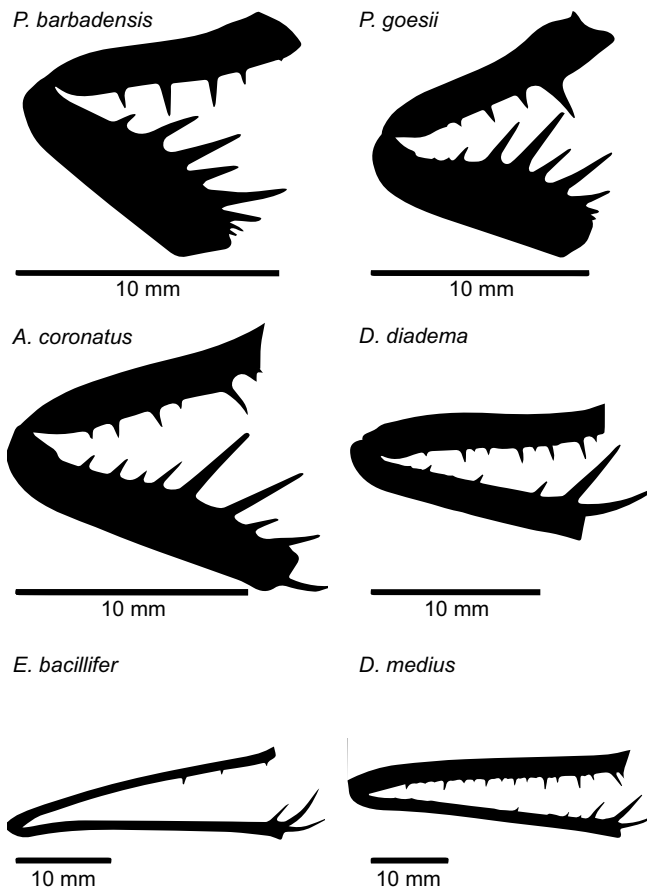


Fig. 2. Outline drawings of the pedipalps of study species in order of total length, showing the large range of sizes and morphologies present in Amblypygi. Study species: *Phrynus barbadensis*, *Phrynus goesii*, *Acanthophrynus coronatus*, *Damon diadema*, *Euphrynichus bacillifer* and *Damon medius*. All pedipalps have been scaled to aid comparison.

the UK and Austria where the research was conducted, and Manchester Metropolitan University guidelines on good research practice.

Filming

Previous anecdotal evidence suggested most Amblypygi taxa hunt nocturnally (Weygoldt, 2000). However, a recent kinematic study of prey capture in amblypygids from the genus *Charon* found the animals to be highly amenable to hunting during daylight (Seiter et al., 2019). Likewise, our preliminary investigations found the individuals studied herein were far more likely to feed in daylight. Prey capture events were filmed from above with a GoPro Hero 5 camera and a 400 Gb microSD card. Events were captured at 240 frames s⁻¹ and 720p quality. The camera was mounted on an adjustable copy stand, with study animals being placed in a prey capture arena below. Two 100 W mercury vapour light bulbs were placed laterally to the arena to provide adequate lighting. The prey capture arena comprised a Perspex box large enough for amblypygids to move freely in (30 cm×25 cm) and a paper substrate with calibration grid. Amblypygids were placed in the prey capture arena and were allowed to acclimatise. Crickets were introduced after an acclimatisation period of 5–10 min. The size of the prey item was roughly scaled to the size of the individual. A total of 86 prey capture events from 23 individuals were recorded across

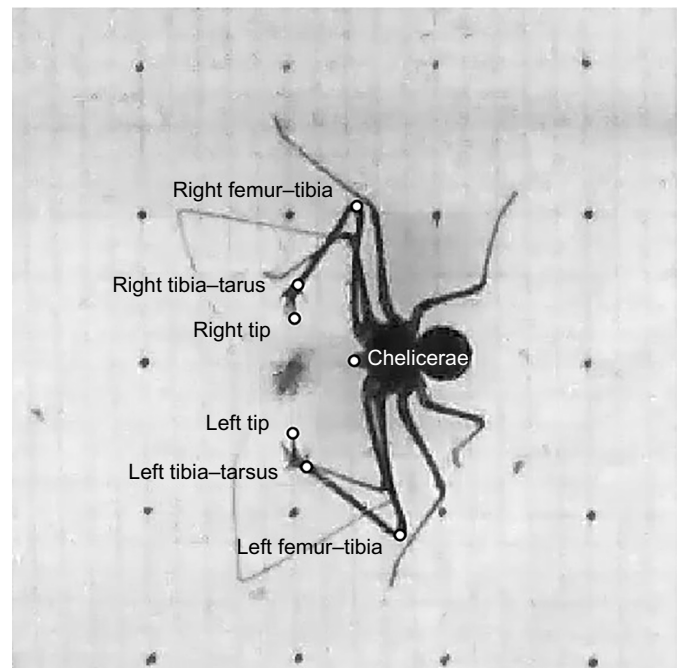


Fig. 3. Location of Amblypygi anatomical landmarks on *E. bacillifer*, tracked from high-speed footage to gather kinematic data during prey capture. The landmark locations are the pedipalp tarsus distal tip, the joint between the tarsus and tibia, the joint between the femur and tibia, and the centre of the chelicerae. Both left and right pedipalps were landmarked.

all species (see Table 1). The minimum spatial resolution of the videos was 0.07 cm pixel⁻¹.

Video and raw data processing

Kinematic data were extracted from the videos by manually tracking the *x,y* coordinates of anatomical landmarks throughout the duration of prey capture using Tracker software (<http://physlets.org/tracker/>). Trials where the pedipalps contacted the side of the Perspex box, and were thus impeded, were removed from the dataset, as were any trials where an amblypygid struck at a prey item but failed to capture and secure it. Some ‘atypical’ trials were also removed *post hoc*, where a prey item jumped directly into the amblypygid’s grasp. Pixel coordinates were converted to metric coordinates using the calibration grid. The landmarks tracked were the pedipalp tarsus distal tip, the joint between the tarsus and tibia, the joint between the femur and tibia, and the centre of the chelicerae. The landmarks were collected for both left and right pedipalps (Fig. 3).

All subsequent data processing, analysis and statistics were performed in MATLAB R2020b (The MathWorks Inc., Natick, MA, USA) with particular use of the Signal Processing Toolbox and Statistics and Machine Learning Toolbox (<https://CRAN.R-project.org/package=signal>; default settings used unless otherwise stated). Raw *x,y* coordinate data were first corrected for slight barrel lens distortion based on the calibration grid, then filtered using a low-pass, zero phase shift, fourth-order Butterworth digital filter (MATLAB ‘butter’ and ‘filtfilt’ functions) with a cut-off frequency of 30 Hz to remove digitisation noise.

To account for out-of-plane movement, a *z* coordinate for all landmarks was calculated. This was achieved by comparing the distance between two landmarks in each frame against the maximum recorded segment length. Any foreshortening present indicates an out-of-plane displacement that can be estimated using trigonometry. The maximum recorded segment length forms the

hypotenuse of a triangle with the foreshortened distance between landmarks as the adjacent side, which allows the angle of the segment to ground plane to be calculated (this may be a positive or negative angle, see below) and a z coordinate assigned for the distal landmark. Maximum segment length was taken as the maximum distance between two landmarks across all trials and was calculated separately for each limb of each individual. Given the joints and associated plane of motion, for this calculation we set the chelicerae to $z=0$, and then assumed the distal femur had positive z values, and that the distal tibia and tarsus were lower than previous segments, dropping away from the camera.

Once z coordinates for all landmarks had been assigned, the data were used to calculate kinematic parameters (Fig. 4). Joint angles between segments were calculated: ‘gape’ angle between the two femora, femur–tibia angle and tibia–tarsus angle. The distance between each tarsus distal tip and the chelicerae, termed ‘reach’, was also calculated. The derivative of reach with respect to time was also calculated to give pedipalp speed (relative to chelicerae). Variables for further analysis were taken during the ‘strike’, which was defined as the time between the first pedipalp starting to close on the prey item (i.e. the first frame with a positive closing speed for either pedipalp) until the last pedipalp finishes closing (i.e. final frame with a positive closing speed for either pedipalp). Within this strike time the variables calculated were, gape angle range, femur–tibia angle range, tibia–tarsus angle range, maximum reach and maximum strike (closing) speed. Angle ranges were defined as the difference between maximum and minimum angles. Maximum

reach was converted to a ratio of maximum reach over total pedipalp length (combined length of femur, tibia and tarsus), termed ‘maximum reach ratio’, which should remain constant across all species if maximum reach is scaling isometrically with pedipalp length. All variables were calculated for both left and right pedipalps.

Data analysis and statistics

A principal components analysis (PCA; MATLAB ‘PCA’ function, with options set to use the correlation matrix) was used to explore the data and test hypothesis 1, that patterns of kinematic parameters (angle ranges, maximum reach ratio, maximum strike speed) are similar across species. All trials for which data were collected were included in the PCA. One-way ANOVA and linear regression models were fitted to maximum reach ratio and maximum strike speed, to test hypotheses 2 and 3. In order to test the ‘maximal’ prey capture performance by the *Amblypygi*, the maximum reach ratio (either left or right pedipalp) and the maximum strike speed (either left or right pedipalp) for each individual across all their trials were selected. One-way ANOVA (MATLAB ‘anova1’ function) were performed with species as the grouping variable, followed by Tukey *post hoc* tests (MATLAB ‘multcompare’ function). For the linear regression models, species averages were taken and regressed against total pedipalp length (combined length of femur, tibia and tarsus). Ordinary least squares (OLS) regressions (MATLAB ‘fitlm’ function) were used as species number in the study was low making phylogenetic corrections impractical and unreliable.

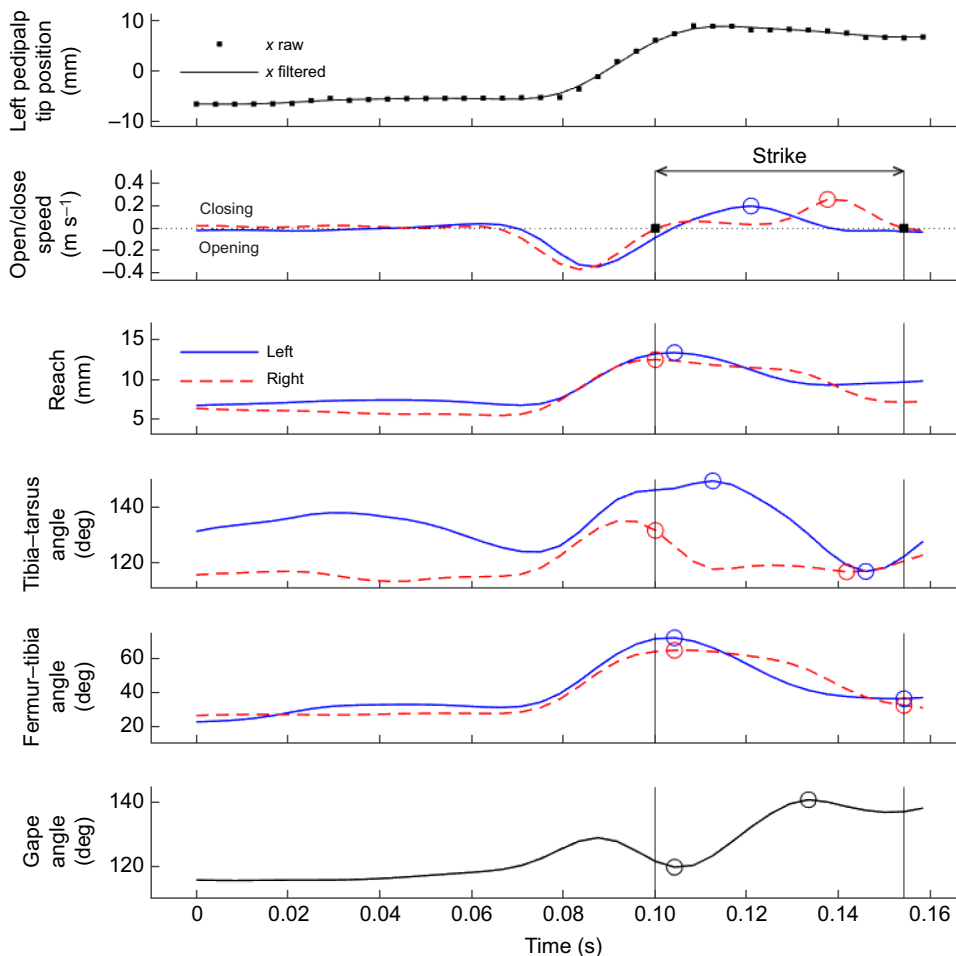


Fig. 4. Example kinematic data calculated from *P. goesii* prey capture landmarks. The strike is defined as spanning from the first pedipalp to start closing on the prey, to the last finishing closing. In this example, both are defined by the right pedipalp (black dots). For the reach and speed data, maximums (circles) during the strike are recorded. For the angle data, maximums and minimums of the strike are recorded (circles), to give an angle range.

RESULTS

Prey capture behaviour

Amblypygi prey capture behaviour has previously been documented in two species (*Charon* sp. and *Phrynus marginmaculatus*) and can be found in Seiter et al. (2019) and Santer and Hebets (2009), respectively. However, a number of behaviours were observed in individuals in our study that differ from the previous behavioural model, and are thus described herein.

The most noticeable difference was in the pre-strike behaviour, which varied markedly between species. Previous work has noted that the pre-strike behaviour in Amblypygi is very consistent, with animals first sensing prey with the whip legs, orienting their body towards the prey item, and slowly opening the pedipalps over a prolonged period at speeds much lower than the rapid closing speeds subsequently exhibited in the prey capture strike (Seiter et al., 2019). The animals then typically use the pedipalps to rapidly strike back at the prey, directing it towards the body (Seiter et al., 2019). However, this pattern was less consistent in our study, with little difference between opening and closing times in *Phrynus* species. This alternative, more rapid pre-strike behaviour was observed in all but three prey capture events within the *Phrynus* species.

Probing with the sensory whip legs was also less common in *Phrynus* species; none was observed in nine of the 32 strikes captured (note, some trials were not included in kinematic analysis as strikes were impeded by the edge of the prey capture arena, or animals failed to capture prey items). Orientation of the body towards the prey also tended to occur after the start of the prey capture strike in *Phrynus*, with 18 of 32 strikes being initiated before the principal axis of the animal's body was in line with the prey. Indeed, our observations showed some pivoting manoeuvres mid-strike in order to orientate the animal towards the prey. Strikes that differed most markedly from the previously reported 'typical' strike behaviour tended to occur when a prey item rapidly approached the amblypygid, especially laterally or from behind the amblypygid. All other species exhibited roughly the behavioural pattern outlined in Seiter et al. (2019), with the main difference between species being the length of the pedipalp opening period, which was much longer in *E. bacillifer* and *D. medius* than in the other species.

Kinematic data

PCA

Species clustering was evident in the PCA of Amblypygi prey capture kinematics (Fig. 5). In particular, species clustered on principal components PC1, PC2 and PC3, which explained 36.4%, 24.5% and 13.8% of the total variance, respectively. PC1 loaded positively with femur–tibia and tibia–tarsus angle ranges. PC2 loaded positively with femur–tibia angle ranges. PC3 loaded strongly positively with gape angle range. Maximum reach ratios and maximum strike speeds did not load strongly with any principal components. In particular, *E. bacillifer* clustered in the bottom left of the PC1–PC2 plot, and to the right of the PC3–PC4 plot, suggesting smaller femur–tibia angle ranges and a larger gape angle range during prey capture. *Damon medius* clustered centrally at the top of the PC1–PC2 plot, indicating potentially larger tibia–tarsus angle ranges compared with other species. Lastly, both the *Phrynus* species clustered somewhat to the left of the PC3–PC4 plot, suggesting use of small gape angle ranges. There was little evidence of clustering by individuals within a species (Fig. 5).

ANOVA

Both one-way ANOVA on maximum reach ratio and maximum strike speed (Fig. 6) showed significant differences between species ($F_{5,17}=10.8$, $P<0.001$ and $F_{5,17}=12.2$, $P<0.001$, respectively). The main species significant differences (Tukey *post hoc* tests, $P<0.05$) were that *D. medius* had a significantly smaller maximum reach ratio than all other species (with the exception of *E. bacillifer*). *Acanthophrynus coronatus* also had a significantly larger maximum reach than *E. bacillifer*. For maximum strike speed, *D. medius* had significantly the fastest strike speed (with the exception of *D. diadema*). *Euphrynichus bacillifer* was also significantly slower than *D. diadema*.

Regression

Linear regression modelling (Fig. 7) found a significant relationship between total pedipalp length and maximum reach ratio ($R^2=0.786$, $F_{1,4}=14.7$, $P=0.0186$). The model fit had a negative slope (-0.165 ± 0.0431 s.e.) such that species with longer pedipalps had significantly shorter reach ratios than species with shorter pedipalps. No significant relationship was found between total

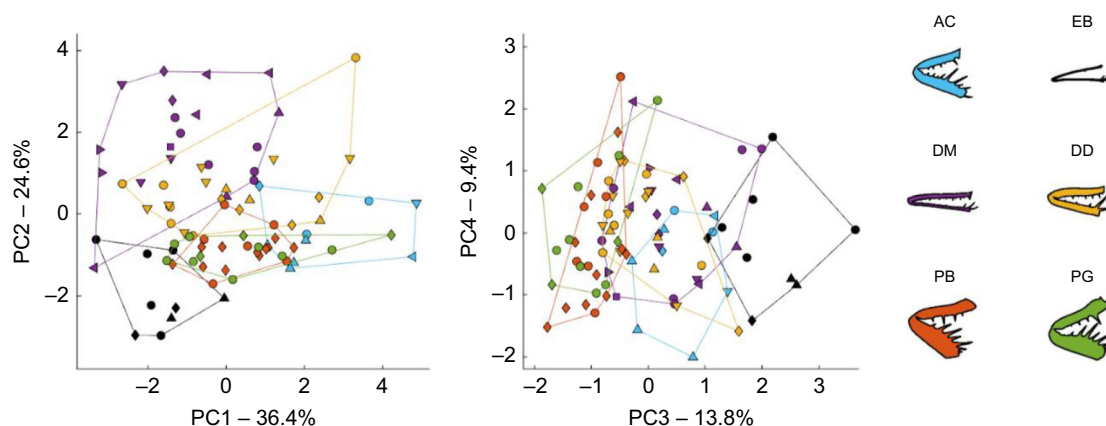


Fig. 5. First four principal components of Amblypygi prey capture kinematics. Species clustering is evident in PC1, PC2 and PC3. PC1 loads positively with femur–tibia and tibia–tarsus angle ranges. PC2 loads mainly positively with femur–tibia angle range. PC3 strongly loads positively with gape angle range. There is no obvious clustering on PC4. Species are indicated by colour (see key, which also shows an outline of their pedipalp morphology: AC, *Acanthophrynus coronatus*; EB, *Euphrynichus bacillifer*; DM, *Damon medius*; DD, *Damon diadema*; PB, *Phrynus barbadensis*; PG, *Phrynus goesii*); individuals are distinguished by symbols. Percentages are total variance explained by each principal component.

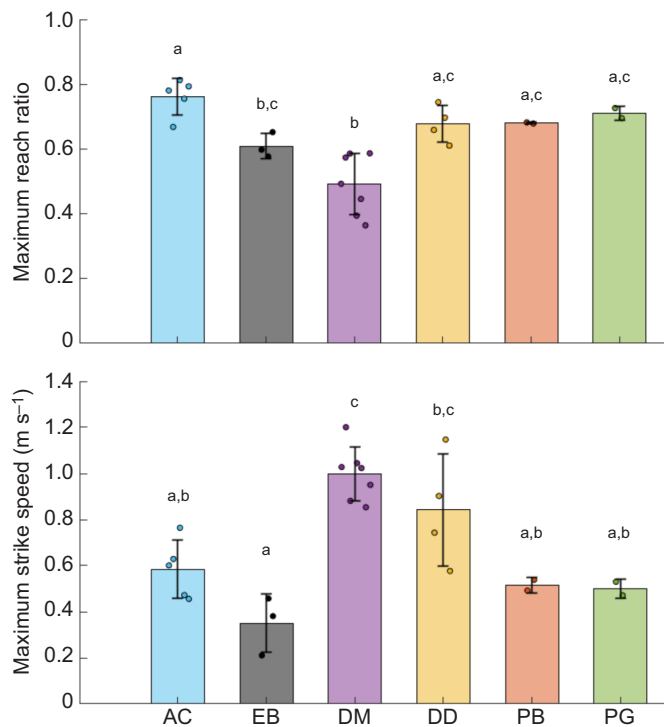


Fig. 6. One-way ANOVA for maximum reach ratio and maximum strike speed. Significant differences were found between species for both parameters. In particular, *D. medius* had significantly the smallest reach ratio (excepting *E. bacillifer*) and fastest strike speed (excepting *D. diadema*). Small circles show the data for each individual. Different letters above standard deviation error bars indicate significant differences between species ($P < 0.05$, Tukey *post hoc* test).

pedipalp length and maximum strike speed ($R^2 = 0.126$, $F_{1,4} = 0.577$, $P = 0.490$), despite a small upward trend being noticeable, with the exception of one species that had the slowest strike speed (*E. bacillifer*).

DISCUSSION

The data presented herein lead us to reject two of our three hypotheses regarding Amblypygi pedipalp kinematics during prey capture. First, we found that basic kinematic parameters do differ significantly between species (Fig. 5), counter to previous anecdotal suggestions (Weygoldt, 2000) and therefore we reject hypothesis 1. Second, maximum reach ratio during prey capture did not remain constant relative to total pedipalp length across species (Fig. 7) and therefore we reject hypothesis 2. We found no evidence, however, to reject our third hypothesis (hypothesis 3) as strike speed during prey capture did not differ significantly relative to total pedipalp length (Fig. 7), despite significant differences between individual species being evident (Fig. 6).

Variation in prey capture behaviour

Prey capture behaviour varied significantly between Amblypygi species: the strategies used in prey capture strikes differed and clustering was evident in a PCA of their kinematic data. This finding was contrary to our expectations (hypothesis 1), which were based on previous observational data from Weygoldt (2000), of consistent prey capture behaviour across species. In particular, the *Phrynosoma* species had similar pedipalp opening and closing times, used their whips less often, and would even reorient their body mid-strike. This differed markedly from the other study species such as

D. medius, which opened their pedipalps slowly and oriented themselves towards the prey item over an extended period prior to the prey capture strike, with the aid of probing with the whips. *Euphrynichus bacillifer* and *D. medius* noticeably clustered away from other species in the PCA (Fig. 5) and appeared to make use of different joint angle ranges during prey capture from other species. Interestingly, these two species both had the longest pedipalps in relation to body size (Table 1), yet also clustered away from each other, particularly on PC2. Furthermore, these two species had significantly different maximum strike speeds, with *E. bacillifer* being slower than either *Damon* species (Fig. 6). This suggests that whilst *E. bacillifer* and *D. medius* both have very long pedipalps, they use them quite differently during prey capture. Indeed, despite being long, the pedipalps of *D. medius* still resemble the basic morphology of other species. In contrast, *E. bacillifer* is a morphologically extreme example of Amblypygi pedipalps (Fig. 2), being thin as well as long, and bearing a reduced number of spines, which may necessitate changes in their prey capture mechanics. Indeed, very few species possess longer pedipalps relative to body size. The kinematic differences reported here raise the intriguing possibility that *E. bacillifer* sits close to a functional limit for the amblypygid pedipalp. Future work may examine prey capture in even more morphologically extreme species such as *Euphrynichus amanica* or *Phrynosoma* species (although we found *E. amanica* unwilling to capture prey while being filmed for the present study). Anecdotal, *E. amanica* feeds very infrequently relative to other amblypygids, perhaps as a result of having a relatively low metabolic rate, suggesting that selective pressures for courtship and display may heavily outweigh those for prey capture (M.S., personal observations). Whether *E. amanica* has modified its prey capture behaviour in light of its extreme appendages remains unknown. Clearly, the relationship between pedipalp morphology and prey capture is much more complex than we predicted and warrants further study.

Maximum reach

The maximum reach ratio of the pedipalps does not remain constant with pedipalp length (Fig. 7), as would be predicted by geometric scaling (hypothesis 2). There is a negative slope to the linear model such that amblypygids with longer pedipalps have smaller maximum reach ratios. Simply put, amblypygids with longer pedipalps are not exploiting this extra length to proportionally extend their reach and therefore longer pedipalps perform ‘worse’ than would be predicted, though they do have a greater reach in absolute terms.

Data concerning Amblypygi feeding ecology are sparse, and mostly observational (particularly in the wild), but the differences we document here may be driven by differences in hunting behaviour. Indeed, our observations of prey capture strategy included differences in species’ behaviour (see also above), particularly that body speed tends to be higher in species with proportionally shorter pedipalps. Indeed, species with shorter pedipalps typically move their whole body towards the prey during the capture strike, whilst those with longer pedipalps keep their body stationary, and the pedipalps alone move towards the prey. Species such as *P. barbadensis* and *P. goesii* appear to begin their prey capture strike further away from the prey item, then move their body forward by extending the fourth leg pair. Unfortunately, absolute distances between predator and prey were difficult to robustly quantify across all species because of the propensity for *P. barbadensis* and *P. goesii* to strike at already moving prey and/or pivot during the strike. Moving toward the prey by extending the

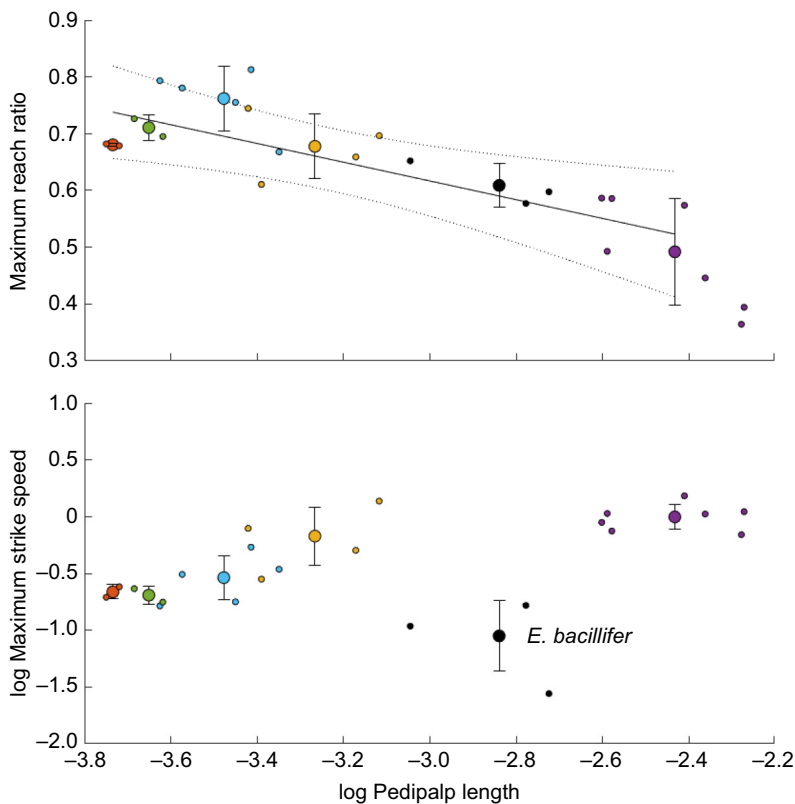


Fig. 7. Linear regression models of maximum reach ratio and maximum strike speed against total pedipalp length. Models used mean species data, shown as large circles. Small circles show the data for each individual. A significant negative relationship was found between reach ratio and pedipalp length (in m), such that species with longer pedipalps had significantly shorter reach ratios. No relationship was found between strike speed (in m s^{-1}) and pedipalp length. The dotted lines indicate 95% confidence intervals on the models and the error bars show standard deviations.

fourth leg pair may be one way in which species with shorter pedipalps compensate for shorter absolute reach than species with longer pedipalps, allowing them to start prey capture from further away from the prey item. Moving beyond the pedipalps, future research should aim to also incorporate kinematics of the body, propulsive leg movements and whip probing, in order to gain a more holistic understanding of species-level differences in amblypygid feeding strategy.

Another reason for the decline in reach ratio could be that species with longer pedipalps are not utilising their full reach, in order to decrease pedipalp closing time. As pedipalp closing speed remains roughly constant across all species, decreasing the distance the pedipalp tip must travel in order to fully close, by not opening the pedipalps as wide, could be an effective way of decreasing closing time. How the exact start and end points of closing are defined is subjective, but anecdotally we note that species with shorter pedipalps appeared to have lower duration pedipalp closing times. Further work on pedipalp closing duration, using higher frame-rate cameras, may shed further light on this hypothesis.

Maximum speed

We found no relationship between pedipalp length and maximum strike speed (Fig. 7), matching hypothesis 3. A general upwards trend is apparent across the species with increasing length, if we assume that *E. bacillifer* is an outlier. However, without more data on species with long pedipalps it is difficult to ascertain whether this is a function of our sampling or a more general trend. Further data collection on Amblypygi prey capture kinematics are needed to clarify this. We did, however, find differences between species (Fig. 6). *Euphrynichus bacillifer* was significantly slower than both *Damon* species, and *D. medius* was significantly faster than all other species except *D. diadema*. This suggests that species differences in strike speed may relate to factors other than pedipalp length.

The lack of an increase in closing speed with increased pedipalp length may, in part, be related to the change in shape that accompanies lengthening of the amblypygid pedipalp. This change nullifies one of the primary assumptions of geometric similarity which states the pedipalp will increase in size in all directions in a similar fashion, rather than just length. Previous pedipalp shape analyses conducted by the authors (McLean et al., 2020, 2021) have identified an inherent shape change associated with increasing pedipalp size, both intraspecifically in *Damon variegatus* and interspecifically across a phylogenetically diverse set of amblypygid species (McLean et al., 2020, 2021). In both cases, lengthening of the pedipalp is accompanied by a narrowing of the femur and tibia perpendicular to the segment long axis and shorter spines (McLean et al., 2020, 2021). *Euphrynichus bacillifer* is an extreme example of this, where the pedipalp central shaft has been reduced to the point where it is narrower in absolute terms than that of species with much shorter pedipalps. This shape change is probably associated with a decrease in the relative physiological cross-sectional area of the pedipalp and the associated musculature within per unit length. Species such as *D. medius* and *E. bacillifer* are therefore expected to possess less pedipalp muscle per unit length, potentially explaining some of the decrease in prey capture ‘performance’ noted herein. We also note that sexual dimorphism in pedipalp size and shape is present in some amblypygid species, with males typically exhibiting longer pedipalps (McLean et al., 2018). Though such differences between sexes are small compared with those between the species studied herein, male amblypygids may well experience a similar but smaller decrease in prey capture ‘performance’ relative to females of the same species for the above reasons. However, further work is required to understand the implication of other shape differences, such as curvature and spination, on prey capture.

General discussion

The rejection of the hypothesis that maximum reach ratio will be constant with pedipalp length suggests that increased pedipalp length is not fully utilised during prey capture. Thus, we suggest that longer pedipalps have evolved under a selective pressure other than optimisation for prey capture. For example, intraspecific contest may also drive the evolution of elongate pedipalps (Weygoldt, 2000; McArthur et al., 2018). Recent work in *P. longipes* has suggested that over 80% of conflicts are decided via display, with the individual that has the longest pedipalps coming out as victor in the vast majority of these cases (Chapin and Reed-Guy, 2017). As territoriality has been observed in a number of amblypygid species (Beck and Görke, 1974; Weygoldt, 2000; Porto and Peixoto, 2013; Chapin and Hill-Lindsay, 2016), and contest behaviour follows a consistent pattern across taxa (Weygoldt, 2000), this may be a common selective pressure across the order. Sexual selection may also be a factor, as pedipalp display is a precursor to mating in the majority of species, and may explain why differences in pedipalp length and shape between males and females tend to present from sexual maturity (McLean et al., 2020). However, it is clear from the interspecific morphology of the pedipalp that a single factor is unlikely to adequately explain the diversity in form present across this order.

Differences in habitat and associated prey availability, or feeding behaviour, will place variable pressures on the feeding apparatus. Feeding ecology, in particular, is an important factor in the development of prey capture devices and could explain the differences in strike speeds between species (Fig. 6). For example, the comparatively longer jaws of the butterflyfish *Forcipiger longirostris* allow for strikes to be initiated at a greater distance from prey items than in other butterflyfish, allowing the species to feed on more elusive prey than close relatives, despite having no advantage in jaw closing speed (Ferry-Graham et al., 2001). Indeed, in vertebrates, decreased strike speed during prey capture can be beneficial; lower swimming speed during prey capture allows greater prey capture accuracy in some fish species (Higham et al., 2006; Higham, 2007; Webb and Skadsen, 1980). Trade-offs between prey capture device length and kinematics are also seen in some other arachnids. For instance, in scorpion palpal chelae or claws, there is a negative correlation between closing speed, which is typically higher in species with longer chelae, and closing force, which is higher in species with shorter chelae (Simone and van Der Meijden, 2017). Species with longer chelae have an advantage in opening gape (Simone and van Der Meijden, 2017). In this context, such a functional trade-off could hypothetically exist in Amblypygi; taxa with long pedipalps might optimise for larger absolute reach and prey capture accuracy, whilst reducing other important prey capture factors, such as manoeuvrability or time to secure prey. Such an effect could reflect differences in feeding ecology between species.

However, data on amblypygid feeding ecology are scant, and no observations of prey capture or diet in the wild have been published on any of the species contained in this study: all are assumed to consume a collection of ground-dwelling invertebrates. There are also few data regarding microhabitat preferences from which one could infer dietary preferences in the species studied. *Damon medius* is known to inhabit termite mounds, though it is unclear how widespread such behaviour is in this species (Chapin and Hebets, 2016). The easy availability of an abundant food resource could decrease the selective pressure on prey capture performance, while allowing energy to be invested elsewhere. Conversely, both *Damon* species and *A. coronatus* have been observed inhabiting caves,

where prey is generally uncommon (Weygoldt, 2000). Intriguingly, cave-dwelling individuals have been observed to have longer sensory ‘whips’ than individuals of the same species that live in the surrounding environment outside the cave (Weygoldt, 2000). As detection of prey is thought to primarily involve the whips and other chemoreceptors and mechanoreceptors, the longer whips may allow cave-dwelling individuals to sense prey at a greater distance. This may in turn create a selection pressure for increased reach during prey capture. However, it is unknown how common cave dwelling is, and thus whether this could lead to a strong selective pressure on a species. Future studies linking quantification of prey capture kinematics with better understood feeding ecologies are key to clarifying the link between diet and function. This could be particularly beneficial in species that differ from the typical amblypygid diet of ground-dwelling invertebrates.

Amblypygi species also appear to markedly differ in their social behaviour, though more research needs to be carried out on this. While the majority of species appear to live a solitary life, group-living has also been observed in a number of taxa (Weygoldt, 2000; Rayor and Taylor, 2006; Chapin and Hebets, 2016). Group size may serve to increase the selective pressure on territoriality and/or sexual selection as the number of interactions with other individuals is likely to be higher in a larger group. This may, in turn, select for larger appendages. For example, the size of male weapons has been found to increase with group size in both bovids and pseudoscorpions (Zeh, 1986; Bro-Jørgensen, 2007). *Euphrynichus bacillifer*, the species with the longest pedipalps relative to body length in this study, is also one of the few Amblypygi species that can successfully be kept communally in captivity (M.S., personal observations). Successful cohabitation is uncommon in the *Damon* species, although it has notably been observed in *D. diadema* in laboratory settings; such aggregations, however, broke down at the onset of sexual maturity (Rayor and Taylor, 2006). Cohabitation is almost completely absent in the *Phrynus* and *Acanthophrynus* species (M.S., personal observations), with the caveat that aggregations of juveniles have been observed in the lab in *Paraphrynus*, thought to be the closest related genus to *Acanthophrynus* (Schramm et al., 2021). The paucity of information regarding Amblypygi behaviour in the wild prevents us from drawing any solid conclusions regarding the effects of social behaviour. Future work on wild social dynamics and feeding behaviour is needed to gain further insights into the selective pressures to which pedipalps are subject. Differences in pedipalp morphology due to ontogenetic changes in shape and relative length of body appendages may also affect prey capture.

Limitations

We note that all relationships predicted using OLS regressions should be treated with some caution, as OLS does not take into account the phylogenetic relationships between species. A group-wide molecular phylogeny of Amblypygi is now available as a preprint (de Miranda et al., 2022 preprint), but does not include several of the species included in the present study. Furthermore, the estimation of lambda for such a small number of taxa is likely to be unreliable (Todorov et al., 2022), rendering the application of modern phylogenetic methods to comparative kinematic studies such as ours problematic.

In future prey capture data collection, placing a camera ventrally and filming prey capture from below may prove informative, as additional proximal pedipalp segments should be distinguishable. We note, however, that caution would need to be taken to find a transparent floor that species lacking pulvilli between their claws

can grip (Seiter et al., 2019). Additionally, filming with multiple cameras to allow full capture of 3D kinematics would be beneficial and remove the necessity of estimating *z* coordinates via the foreshortening of segment lengths.

We also note that this study contains a mixture of wild-caught and captive-bred specimens. Specimens that have been captive bred can be more docile than their wild-caught counterparts and it is possible that this could result in some differences in prey capture behaviour.

Conclusion

Here we show that, contrary to our hypotheses, geometric scaling does not adequately describe the kinematics of prey capture in Amblypygi with differing pedipalp lengths. Instead, we found that prey capture kinematics differ markedly between species. In particular, species with relatively longer pedipalps have a reduced maximum reach ratio. In essence, species with longer pedipalps are not fully utilising their potential reach. Rather, we posit that long pedipalps may have evolved under different selective pressure from simply a mechanical advantage during prey capture, with territorial contest and sexual selection being potential candidates for driving extreme morphologies. Further research into wild amblypygid behaviour is needed to explore the relative importance of these behaviours. Our work documents the form–function relationship present within the unique system of the amblypygid pedipalp, and highlights potentially complex interactions between morphology, prey capture and the intriguing social dynamics of this enigmatic group of arachnids.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: C.J.M., C.A.B., R.J.G.; Methodology: C.J.M., M.S., J.D.G.; Validation: J.D.G.; Formal analysis: C.J.M., J.D.G.; Investigation: C.J.M., C.A.B., M.S.; Resources: M.S.; Data curation: C.J.M.; Writing - original draft: C.J.M.; Writing - review & editing: C.A.B., M.S., R.J.G., J.D.G.; Visualization: C.J.M., J.D.G.; Supervision: C.A.B., R.J.G.; Project administration: C.J.M., C.A.B., R.J.G.; Funding acquisition: C.A.B.

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Data availability

Prey capture videos, tracker data and code for processing and analysis of kinematic data are available from figshare: <https://doi.org/10.6084/m9.figshare.25013771.v1>

ECR Spotlight

This article has an associated ECR Spotlight interview with Callum McLean.

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